SOME PROCESSES INVOLVED IN THE WIND SHAPING OF CONIFER TREES

by

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Frontispiece. A wind shaped larch growing on Turnhouse Hill, Midlothian, Scotland.

TABLE OF CONTENTS

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ABSTRACT

This thesis reports a four year study to investigate the cause of wind-shaping in trees. The main study site was a Sitka spruce plantation at Dunslair Heights, Scotland. The fates of individual shoots were followed over the study period. Shoot breakage occured mainly during the season of active extension growth in strong winds. Windward shoots were broken much more often than leeward shoots. Surviving shoots on the windward side displayed strong curvature, the extent of curvature for more sheltered shoots being less. A parallel experiment in the greenhouse showed that deflections applied for only a few hours each day were 'fixed' if the deflections were applied during the stage of growth when the stem is hardening. In the field the extension rates of terminal shoots were also measured. The largest length increments were recorded on leeward branches, arising each year from their larger initial bud size, in comparison with the buds on the windward branches.

The energy balance of shoot apices was considered in relation to the possible temperatures of the buds and apices. Preliminary measurements of these temperatures were made on Arolla pine at the tree-line in the Austrian alps; and later, more extensive measurements were made on Sitka spruce at Dunslair Heights. A maximum difference of 5°C between sheltered and exposed shoots was recorded. Such maxima occured at high solar irradiance and low wind speed. A subset of the data was used to estimate boundary layer resistances of sheltered and exposed shoots. The significance of the temperature difference as a causative agent in asymmetry of the tree is discussed.

In a parallel experiment in the greenhouse an attempt was made to apply a gradient of surface temperature across the canopies of young trees by using radiative heat transfer. Despite technical difficulties in simulating an ecologically realistic regime, the warmed shoots did achieve greater extension not only in the year of treatment but in the following year as well. Finally, the relative importance of the various processes is considered, and areas for further study are identified.

CHAPTER 1
INTRODUCTION

Wind-shaped trees occur in places where high winds are frequent and tend to blow mainly from one direction. The characteristic feature of these trees is asymmetric canopy development, the branches of the leeward (sheltered) side being longer than those of the windward (exposed) side, which are sometimes completely absent. Often the branches are swept back, so that they point away from the prevailing wind direction and most of the foliage occurs to the leeward of the stem. The term, 'flag-tree', is often used to describe wind-shaped trees and aptly conveys their appearance. A particularly extreme example is shown in the frontispiece.

Much attention has been given to these dramatic components of the landscape, although most of the work on wind-deformed trees has been largely descriptive. The axis of maximum asymmetry of the wind-shaped crowns is considered a good indicator of prevailing wind direction, so surveys of flagged trees have been undertaken to investigate the flow patterns of the surface wind over large areas of terrain. These studies include those of Sekiguti (1951) in Nagano Prefecture, Japan; Thomas (1958) in Cardiganshire, Wales; Oliver (1960) in Pembrokeshire, Wales; Holroyd (1970) in New York State, U.S.A.; Plesnik (1973) in the Rocky Mountains of the U.S.A.; Yoshino (1975) in Japan and eastern Europe; and Noguchi (1979) in Hawaii.

In addition to their use as indicators of wind direction, wind-shaped trees have also been used to assess mean annual wind speed. The first classification of wind effects on the shapes of trees was the Griggs-Putnam index. This was developed by R.F.Griggs, who collaborated with P.C.Putnam in a survey of New England, U.S.A., designed to locate sites suitable for the installation of wind turbines for generating electricity (Putnam, 1948). The Griggs-Putnam index is a subjective scale used to classify the crown response of conifers (or other conically-shaped species) to the prevailing wind conditions. Diagrams showing the eight grades of crown shape, ranging from no wind-effect to extreme deformation, are reproduced in figure 1.1. Later, Barsch (1963) devised a similar index for broad-leaved trees. A further, more complex, classification was proposed by Yoshino (1975).

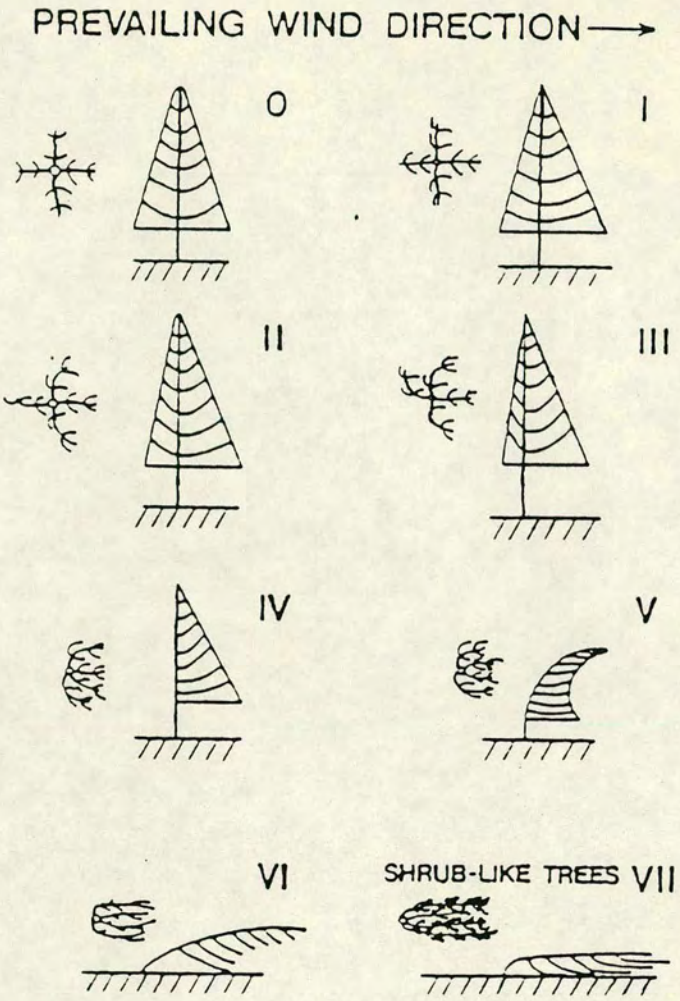


Figure 1.1. Wind deformation in conifer trees characterized by the Griggs–Putnam index (from Wade and Hewson, 1980).

The above indices of tree deformation were only related to wind speed in a semi-quantitative manner. The first attempt to establish a quantitative relationship was made by Owada (1973). He used Yoshino's classification to grade Japanese larch (*Larix leptolepis*) trees and calculated a linear regression to relate deformation to measurements of mean growing season wind speed. The most extensive work of this type was done by Wade and Hewson (1980). They 'calibrated' numerous species, mostly from the western U.S.A., by calculating linear regressions between four different indices of deformation and meteorological records of mean annual wind speed at 120 locations.

Despite this wealth of descriptive work, little is known about the processes involved in the deformation of tree crowns, although there has been some speculation, which will be discussed subsequently. Noguchi (1979) observes that:

> "there is clearly a need for more exact answers to the mechanism of deformation through more detailed field observations and long-term physiological experiments."

It is the objective of this thesis to satisfy this need to some degree, by detailed investigation of several different processes thought to be involved.

Wind-shaped trees are most frequently seen close to the coast or at high altitudes, as it is in these regions that high mean annual wind speeds are observed (Grace, 1977). In coastal areas tree deformation results largely from the impaction of windborne salt particles on the leaf surfaces. At Cape Fear, North Carolina, Wells and Shunk (1937) showed that deformation along the coast was largely the result of salt damage, rather than wind alone. The field measurements reported in this thesis were made at sites distant from the coast, where salt plays no role in the wind-shaping process.

The most obvious effects of wind on trees are mechanical ones. Wind damage includes breakage of branches or leaves, abrasion and defoliation. These effects can be caused by both persistent strong winds and occasional severe winds (Wade and Hewson, 1979).

The season during which most mechanical damage occurs seems to depend on the climate. In regions with an alpine or sub-alpine climate, where

winters are very cold, the accumulation of heavy deposits of ice 'glaze' on exposed branches, eventually resulting in their breakage, is thought to be the primary cause of wind-shaping (Lawrence, 1939). As high winds buffet the frozen, ice-covered branches, they rub together, causing abrasive damage to their surfaces (Marchand, 1980). Surface damage also results from blasting by windborne ice (Daubenmire, 1959) or soil (Grace, 1977) particles.

Winters are less severe in oceanic climates, however, and most breakage occurs when the fragile new shoots are produced (Thomas, 1958). Wilson (1978) found that the leaves of sycamore (*Acer pseudoplatanus*) were particularly vulnerable to damage during the period of expansion and described surface lesions, indicative of damage caused by mutual abrasion between leaves moving in the wind. Disruption of the cuticle and epidermis causes high rates of evaporative water loss, encouraging water stress, which is deleterious to shoot growth.

The force of the wind against the exposed side of the tree tends to hold the branches in a swept back position, so that their apices face away from the wind. Putnam (1948) suggested that an important process in wind deformation was the occurrence of lignification while the still-flexible young shoots were swept back by the wind. A similar observation was made by Holroyd (1970).

Gusting of the wind causes motion of the tree's stem and branches, which can induce morphological changes. Larson (1965) compared the growth of tamarack (*Larix laricina*) trees that had been staked to prevent wind sway with others left to move freely in the wind. The unsupported trees grew less in height, but more in girth, than the staked ones. Trees exposed to strong winds from one quadrant develop asymmetrical radial growth in the lower trunk due to the formation of compression wood. Wade and Hewson (1980) measured the asymmetry in annual ring widths ('compression ratio') and found it to be linearly related to mean annual wind speed for a variety of species. The adaptive significance of these changes seems to be to confer additional strength to the tree.

Several authors (Neel and Harris, 1971; Rees and Grace, 1980) have presented results which indicate that shaking *per se* causes a reduction in height growth. These observations suggest that shaking might be partially responsible for the low stature of wind-shaped trees. If the windward

branches of the tree experience more shaking than those of the leeward side, then motion-induced growth reduction might also be involved in the formation of asymmetrical crown shapes.

The desiccation of exposed shoots has been implicated in the wind-shaping of trees. Daubenmire (1959) suggested that trees exposed to severe winds in mountainous regions may lack branches on their windward sides due to the killing of buds in the winter by desiccation. Wardle (1968) also discussed the importance of desiccating winds under severe winter conditions as a possible cause of tree deformation. On clear, sunny days, with drying winds and frozen soil water, shoot water potential is liable to fall to lethal levels, as evaporative water losses cannot be replaced by uptake.

Tranquillini (1974) observed that the 'browning' of Norway spruce (*Picea abies*) shoots (resulting from death caused by winter desiccation) is particularly prevalent in the spring following a cool summer. The trees he studied grew close to the altitudinal tree-line, where growth is strongly limited by the duration of favourable summer temperatures. During a poor summer, the shoots are unable to finish their growth properly before dormancy. Their incompletely developed cuticle has a low resistance to water loss, so they experience particularly severe damage in the following winter. This effect might be especially pronounced for the windward shoots, as there is some evidence (reviewed later) to suggest that, during the growing season, they generally experience lower temperatures than the sheltered ones.

The role of water relations during the growing season in the wind-shaping of trees is unclear. Daubenmire (1959) proposed that wind affects plants by promoting transpiration rate, thus inducing water stress. As the windward shoots of a tree are exposed to a greater wind speed than sheltered ones, they might be expected to experience lower water potentials, if this suggestion were true. Some supporting evidence is provided by the work of Satoo (1962), who studied the water relations of Hinoki cypress (*Chamaecyparis obtusa*) forming a wind-break near Tokyo. He found that the water content of the leaves was always greater on the leeward side, although the transpiration rate of the windward shoots was only slightly higher than that of the sheltered ones.

The consensus of more recent work is that wind has only a minimal, or even opposite, effect on transpiration. The theoretical calculations of Grace (1981) show that wind often has little influence and may sometimes decrease the rate of transpiration, by lowering leaf surface temperature and thus reducing the driving gradient for evaporation. Dixon and Grace (1984) studied the evaporation from four tree species in a controlled environment wind tunnel, finding in all cases that transpiration rate declined with increasing wind speed. The same result was obtained by Yamoaka (1958) in his study of water loss from from a forest of Japanese red cedar (*Cryptomeria japonica*). Thus it seems likely that the only way wind can increase the transpiration rate of exposed shoots is by causing damage to the epidermis, rather than by a direct effect on the process of water transfer from the leaf to the atmosphere.

Grace (1977) suggested that another possible explanation for the asymmetrical growth of wind-shaped trees might be a difference in surface temperature between their leeward and windward sides. The leeward shoots might simply grow at a faster rate than the windward ones, thus producing an asymmetrically-shaped crown. Gates (1980) put forward the same explanation and claimed to have measured a temperature difference of 9 °C between the sheltered and exposed sides of Engelmann spruce (*Picea engelmannii*). Wade and Hewson (1979) reported that the needles on the leeward side of wind-shaped conifers are often twice as long as those on the windward side. As needle length is known to be strongly influenced by the temperatures experienced during the growing season (Mikola, 1962), their observation also suggests the existence of an appreciable temperature difference. Further evidence supporting this view is discussed in section 5.1, and a consideration of the energy balance theory, leading to the expectation of a temperature difference between windward and leeward surfaces, is presented in section 5.1.1.

If the shoots on the side of the tree that is sheltered from the prevailing wind are indeed warmer than the exposed ones, then it seems reasonable to suggest that they will grow faster, thus producing an asymmetrical canopy. The growth of all plants is slow at temperatures close to 0 °C and increases rapidly with temperature, up to a maximum value, which for temperate species is commonly between 20 °C and 35 °C (Sutcliffe, 1977). The primary factor limiting tree growth at high altitudes, where wind-shaped trees often occur, is

low temperature (Daubenmire, 1954; Wardle, 1968; Tranquillini, 1979; Norton, 1984). The same is true in cold, sub-arctic latitudes (Hustich, 1947; Mikola, 1962). In such environments where ambient temperatures are close to the threshold below which growth cannot occur, a small increase of a few degrees Celsius in mean temperature has a profound influence on growth. As well as causing an increase in growth rate, the length of the growing season may be greatly extended (Jones, 1983). The time of bud opening is also strongly influenced by temperature; this is shown by the good correspondence between year-to-year variations in temperature and the time of growth initiation of a given species in a specific area (Kozlowski, 1971).

In summary, if the sheltered shoots are warmer than the exposed shoots for much of the time, they are likely to benefit by faster growth, and possibly by both a longer period of activity and earlier bud break, if there is some degree of independence between different parts of the same tree. Such enhancement of the sheltered shoots' growth would result in the asymmetrical crown shapes that are typically observed in windy areas.

Some of the possible mechanisms of wind-shaping, introduced above, have been investigated during this study, using three conifer species, Sitka spruce (*Picea sitchensis*), Arolla pine (*Pinus cembra*) and Scots pine (*Pinus sylvestris*).

Chapter 2 describes detailed field observations, over a period of several years, of mechanical wind effects on trees. The study encompassed shoot breakage, the mutual abrasion of shoots and wind-induced bending. The relationship between these effects and shoot orientation, with respect to prevailing wind direction, was investigated.

In chapter 3 a simple experiment conducted to investigate the degree of bending required to produce the permanent fixation of curvature in young shoots is reported. Extending shoots received different bending treatments, intended to simulate wind-induced flexure.

Chapter 4 describes field work, undertaken over a period of several years, to examine the relationship between shoot growth rates and their degree of exposure to the wind.

Chapters 5 and 6 are concerned with attempts to measure the temperature differences between windward and leeward shoots and to examine their relationship to other microclimatic variables. Chapter 5 describes measurements made close to the tree-line in the Austrian alps, while chapter 6 reports a more extensive series of measurements made at an upland site in Scotland.

In chapter 7, a controlled experiment intended to establish a causal link between temperature differences and asymmetrical tree growth is described.

The overall conclusions of this investigation of some wind-shaping processes are presented in chapter 8.

CHAPTER 2
FIELD MEASUREMENTS OF MECHANICAL WIND EFFECTS

2.1. Introduction

The mechanical effects of wind on trees have been outlined in chapter 1. This chapter reports detailed field measurements of some of these mechanical effects, spanning a period of four years. The effects investigated were shoot breakage, shoot damage by mutual abrasion, and the permanent bending of shoots by the wind. The objective was to study the time course of these effects and their relationship to the degree of exposure to the wind experienced by a shoot. Mechanical effects can only play a role in the wind-shaping of trees if they are experienced more frequently by the shoots on the side of the tree exposed to the prevailing wind.

Conifer trees provided a convenient system for study as their growth form is naturally regular. Every year a new whorl of branches grows at the apex of the tree, and the branches of existing whorls increase in length. The branches of each whorl grow (roughly) in a horizontal plane, each branch pointing in a different horizontal direction. It is thus easy to relate the damage or bending experienced by a branch to its orientation relative to wind direction.

In addition to the field measurements, the positions adopted by the shoots of a potted tree at different wind speeds were briefly investigated in a controlled environment wind tunnel.

2.1.1. Description of the site of field measurements

The field site was situated on a north-facing slope (aspect of 336°, slope of 7°), close to the summit of Dunslair Heights, at an elevation of 610 m above sea-level. Dunslair Heights (55° 41′ N, 3° 8′ W) lie to the north-east of Peebles, Peeblesshire, Scotland, at a distance of 5 km (figure 2.1 is a map of the locality).

The trees used for the measurements were Sitka spruce (*Picea sitchensis*), of Queen Charlotte Island provenance, selected within a plantation established in 1971. Prior to planting the ground was ploughed in the direction of the slope, and the trees were planted on the ridges of soil. As a result of the

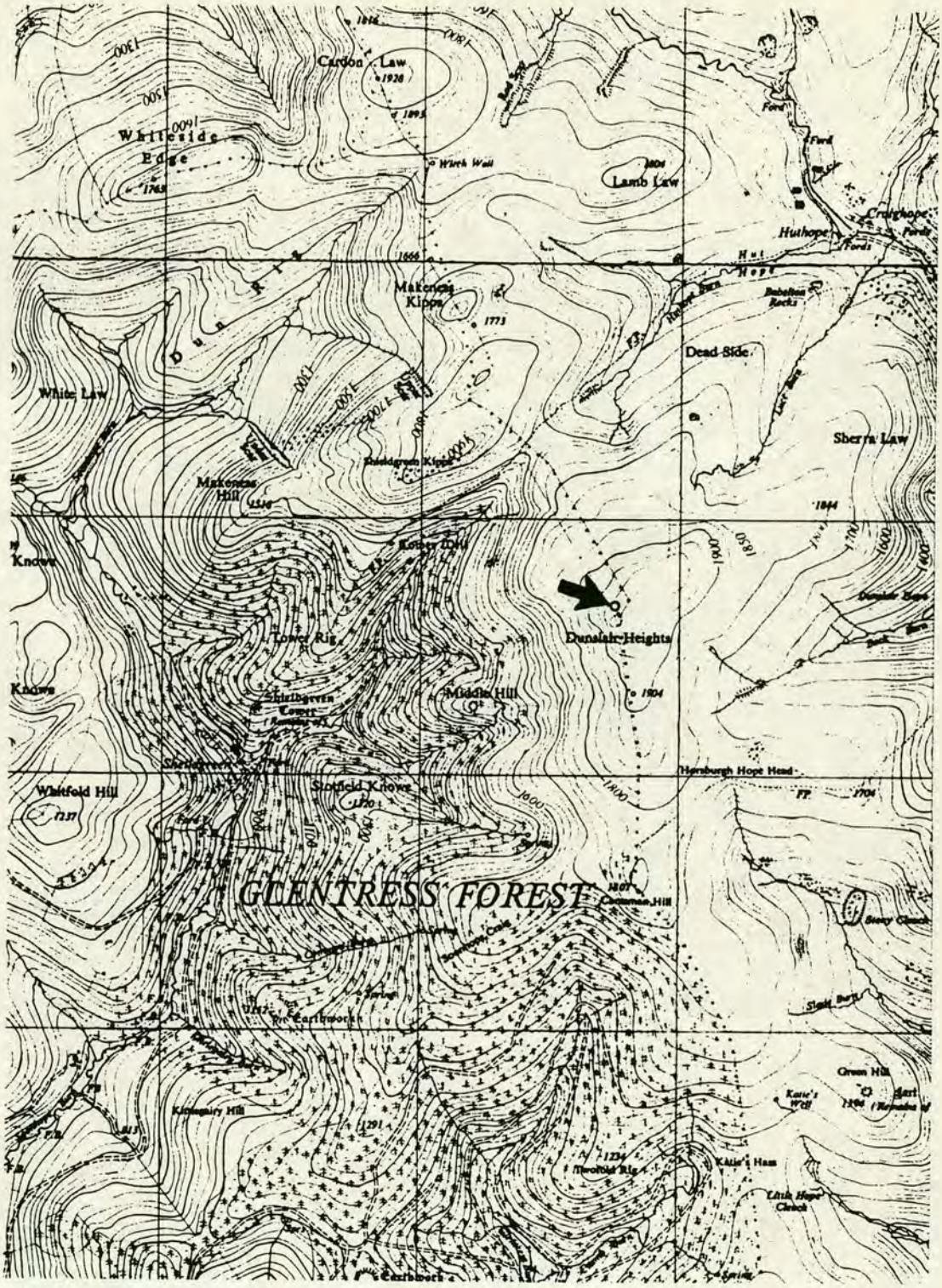


Figure 2.1. Map showing the area around Dunslair Heights, Peeblesshire, Scotland. The location of the field site is marked with an arrow. Scale 1:25000.

exposed nature of the site, which is higher than any of the neighbouring hills, percentage establishment was poor. In 1985, the tallest trees were 2.5 m high, the mean height being about 1.5 m, and the stand density was 2000 stems ha^{-1}. The stand was open, with large gaps separating the trees from one another (see plate 6.1). The trees were visibly wind-deformed, with Griggs-Putnam indices ranging from 2 to 4 (see figure 1.1). The direction of maximum crown asymmetry suggested that strong winds generally blew from the western quarter.

2.2. Methods

Early in 1981, 17 trees were selected for study. Each tree was uniquely numbered with a permanent tag, and a stake was erected nearby to aid re-location. The trees chosen were taller than average (about 1.5 m in 1981) and of vigorous appearance. Individuals whose leading shoot had been lost at some time in the past were excluded from the selection.

The topmost whorl of shoots (which were one year old, having begun their growth in 1980), and the whorl of buds around the apical bud at the end of the leading shoot (destined to form a whorl of shoots during 1981) were selected for the detailed study of wind damage. These two whorls are subsequently referred to as, respectively, the '1980 whorl' and the '1981 whorl'.

The orientation of each shoot or bud with respect to magnetic north was determined with a compass. It was possible to determine the direction towards which each shoot of the 1980 whorl pointed with an accuracy of a few degrees, simply by aligning the edge of the compass with the shoot axis. It was a little more difficult to measure the direction towards which the buds of the 1981 whorl pointed, but it was still easy to uniquely identify each bud by its compass direction. For the purposes of later analysis of the results of the study, the orientations of the shoots of the 1981 whorl were measured again at the end of the growing season, when a more accurate determination of the directions in which they pointed was possible.

Of key importance to the future shape of the tree are the shoots formed from the terminal buds of its branches. If one of these terminal shoots is lost before it has completed its growth (and set the terminal bud that will grow next year) then the branch will cease to grow in length. Thus, it was

considered most important to record the damage experienced by terminal shoots of the 1980 and 1981 whorls (N.B. each branch of the 1981 was only composed of a single, 'terminal' shoot). It was decided, however, to also record damage to the sub-terminal shoots which grow out from the ring of buds around the terminal bud. These shoots are next in size and photosynthetic activity, after the leading shoot and the branch terminal shoots (Leverenz, 1981), so their damage or loss significantly affects the growth of the tree.

The site was visited at intervals during the 1981 growing season, and the shoots under study were scored for damage or breakage. Each shoot was individually identifiable by its compass direction. The sub-terminal shoots were identified by their position on an imaginary clock face when viewing each shoot from its distal end. The degree of damage by the mutual abrasion of shoots was scored on the following scale, by subjective assessment:

Needles lost or damaged (<10%) = 1
10% to 25% of needles lost or damaged = 2
25% to 50% of needles lost or damaged = 3

Damage and breakage occurring to the extending terminal and sub-terminal shoots of the same whorls were also recorded at intervals during the growing season of 1982. In this year, on-site measurements of wind speed and direction were made. The run-of-wind between visits was recorded with a cup-counter anemometer (Meteorological Office; mark II anemometer), allowing the calculation of weekly mean wind speed. Wind direction was sensed with a home made wind-vane. The output of the vane was recorded for one minute in every hour, using a small, battery-powered chart recorder (Grant Instruments Ltd,. Cambridge; model 3D20B). From this data, the daily mean direction was calculated.

To back up some field observations of the mechanics of shoot breakage in high winds, a brief study was made using a wind tunnel. A camera was positioned vertically above a potted Sitka spruce (four years old, from seed) which was exposed to a range of wind speeds up to 12 m s^{-1} in the tunnel (described by Thompson (1975)). At each wind speed, photographs were taken to record the configuration of the tree's shoots.

A final visit was made to the site in June 1985. The same branches as studied previously were examined to see how many had lost their terminal shoots since the end of the 1982 growing season. The direction in which each of the remaining terminal shoots was pointing was measured with a magnetic compass. These measurements were compared with the initial directions of the branches, recorded in 1981, to determine the angle of permanent bending that had been induced by the prevailing wind.

The objective of these studies was to examine the relationship between the occurrence of mechanical wind effects and the degree of exposure experienced by a shoot. To allow analysis of the data collected in a manner designed to achieve this goal, it was necessary to determine the prevailing wind direction as accurately as possible. As there were no meteorological records for the site, the direction of maximum canopy asymmetry was measured, using a magnetic compass, for a sample of trees. This is considered a good indicator of prevailing wind direction (see chapter 1).

2.3. Results

To allow assessment of the relationship between the degree of shoot exposure and the mechanical effects of wind experienced, four 'whorl quadrants' were defined. The limits of these quadrants are shown in figure 2.2, and were defined in relationship to the prevailing wind direction, determined in 1985 from tree deformation. The measurements of tree deformation provided an estimate of 293.7° ±2.6° (mean and 95% confidence limits, N = 14) for prevailing wind direction. This estimate agreed well with the wind speed and wind direction data collected on 130 days in the summer of 1984 (see chapter 6). Figure 2.3 is a plot of these data, and clearly shows that almost all winds of speeds greater than 5 m s^{-1} came from directions very close to that determined from tree deformation.

Quadrant 1 is bisected by the apparent prevailing wind direction, so shoots occupying this quadrant experienced maximum exposure to the wind. The shoots of the opposite quadrant, number 3, experienced least exposure, as they benefitted from the shelter afforded by the rest of the tree's foliage. The shoots in quadrants 2 and 4 experienced an intermediate degree of exposure.

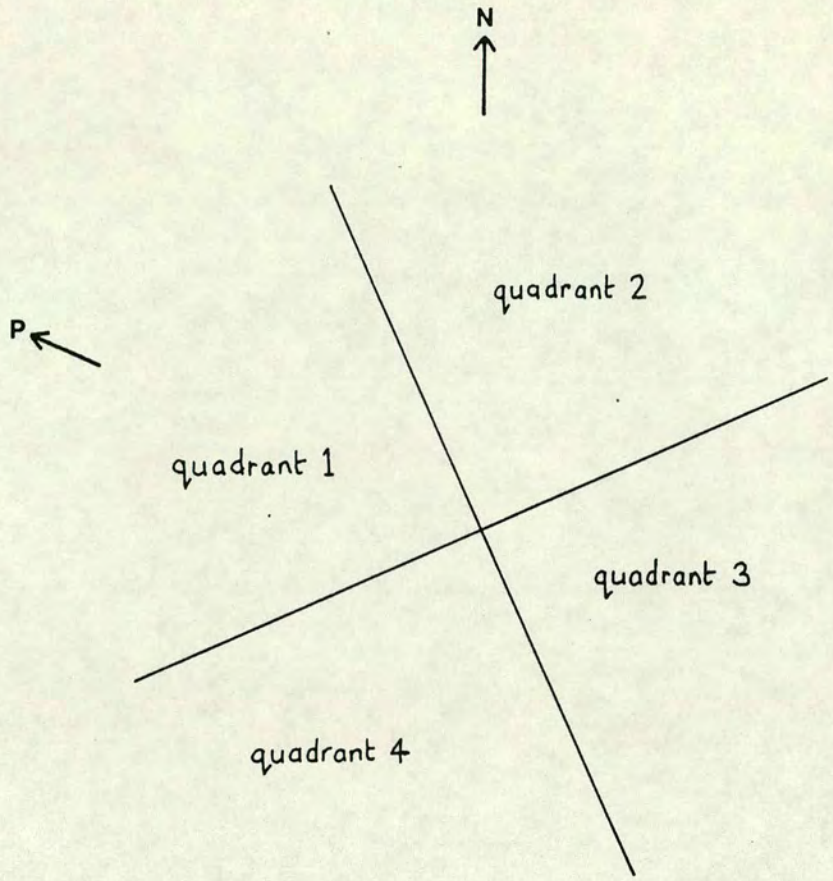


Figure 2.2. Diagram showing the limits of the whorl quadrants used in chapters 2 and 4 to relate measurements of shoot damage and growth to prevailing wind direction. 'N' indicates magnetic north and 'P' indicates the prevailing wind direction (as determined from tree deformation).

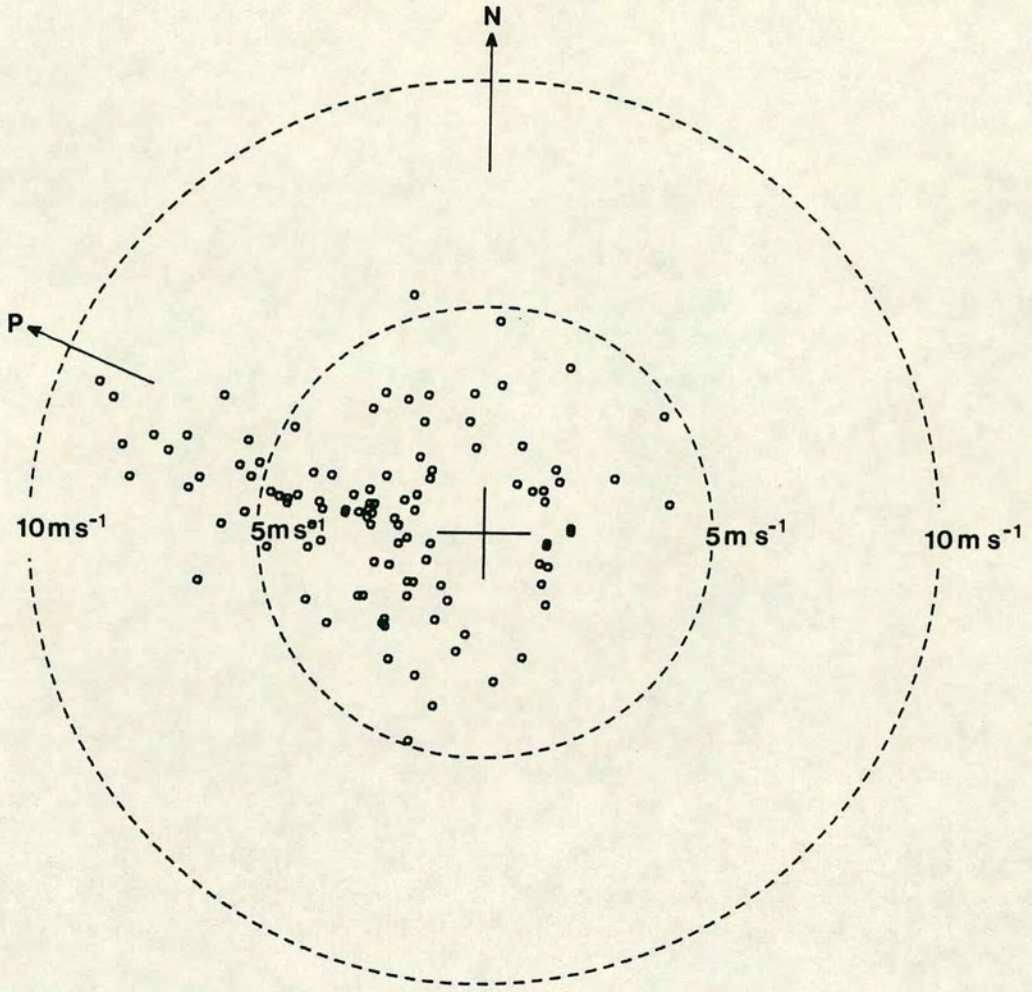


Figure 2.3. Diagram showing wind speed and direction data collected at Dunslair Heights from 14 June to 29 September 1984. Each point represents one day's data: its distance from the centre of the diagram gives the day's mean wind speed, and the direction of its displacement gives the day's mean wind direction, determined from tree deformation.

2.3.1. Shoot breakage

The shoot breakage data for 1981 are given in table 2.1 (terminal shoots) and table 2.2 (sub-terminal shoots). The cumulative count of broken shoots in each quadrant for the 1980 and 1981 whorls of all trees sampled is given at different times during the growing season.

The first breakage of shoots occurred between 17 June and 1 July, by which time, the shoots had achieved about half their final lengths (see figure 4.1). Most shoot breakage occurred in quadrants 1 and 4. By 17 August, by which time extension was complete, 9% of terminal shoots in quadrant 1 had been broken, 7% in quadrant 4 and none in quadrants 2 and 3. The equivalent figures for the sub-terminal shoots were, 10% in quadrant 1, 5% in quadrant 4, 3% in quadrant 2, and 2% in quadrant 3.

The shoot breakage data for 1982 are given in table 2.3 (terminal shoots) and table 2.4 (sub-terminal shoots). Measurements of wind speed and direction were made during the 1982 growing season; these data are plotted in figure 2.4.

As observed during 1981, no breakage occurred during the early period of shoot extension. The first breakages occurred between 10 June and 24 June, by which time the shoots had achieved approximately two-thirds their final lengths (see figure 4.2). During this period there were strong winds from the east (see figure 2.4). Most shoot breakage occurred at this time, in quadrant 3, which contained the east-facing shoots. Little further breakage occurred during the remainder of the growing season. By 14 September, at which time extension was complete, 15% of terminal shoots in quadrant 3 had been broken, while only one had been broken in each of the other quadrants. At this time, 13% of the sub-terminal shoots in quadrant 3 had been broken, while only 3% to 4% had been broken in the other quadrants.

Table 2.5 gives data laid out to show the fates of the branches from the start of the investigation in May 1981 until the final visit to the site in June 1985. Considering both whorls together, by June 1985, a total of 50.9% of branches had lost their terminal shoots or been broken. The data from the first two years of the study suggest that almost all of the breakage occurs during the summer months, rather than in the wintertime.

Table 2.1

cumulative counts of broken terminal shoots in 1980 and 1981 whorl quadrants, determined on various days during 1981; data from 17 trees.

		Cumulative broken shoot count							
Quadrant number	Number of shoots	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1	35	0	0	0	0	1	3	3	3
2	43	0	0	0	0	0	0	0	0
3	44	0	0	0	0	0	0	0	0
4	45	0	0	0	0	0	2	3	3

Table 2.2

Cumulative counts of broken sub-terminal shoots in 1980 and 1981 whorl quadrants, determined on various days during 1981; data from 17 trees.

		Cumulative broken shoot count							
Quadrant number	Number of shoots	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1	60	0	0	0	0	5	6	6	6
2	92	0	0	0	0	0	1	2	3
3	102	0	0	0	0	0	1	2	2
4	97	0	0	0	0	1	3	4	5

Table 2.3

Cumulative counts of broken terminal shoots in 1980 and 1981 whorl quadrants, determined on various days during 1982; data from 15 trees.

		Cumulative broken shoot count						
Quadrant number	Number of shoots	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22	Sep 14
1	30	0	0	0	1	1	1	1
2	42	0	0	0	1	1	1	1
3	47	0	0	0	5	7	7	7
4	39	0	0	0	0	0	0	1

Table 2.4

Cumulative counts of broken sub-terminal shoots in 1980 and 1981 whorl quadrants, determined on various days during 1982; data from 15 trees.

		Cumulative broken shoot count						
Quadrant number	Number of shoots	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22	Sep 14
1	99	0	0	0	0	0	0	4
2	143	0	0	0	2	3	3	5
3	160	0	0	0	12	15	15	20
4	137	0	0	0	0	2	2	4

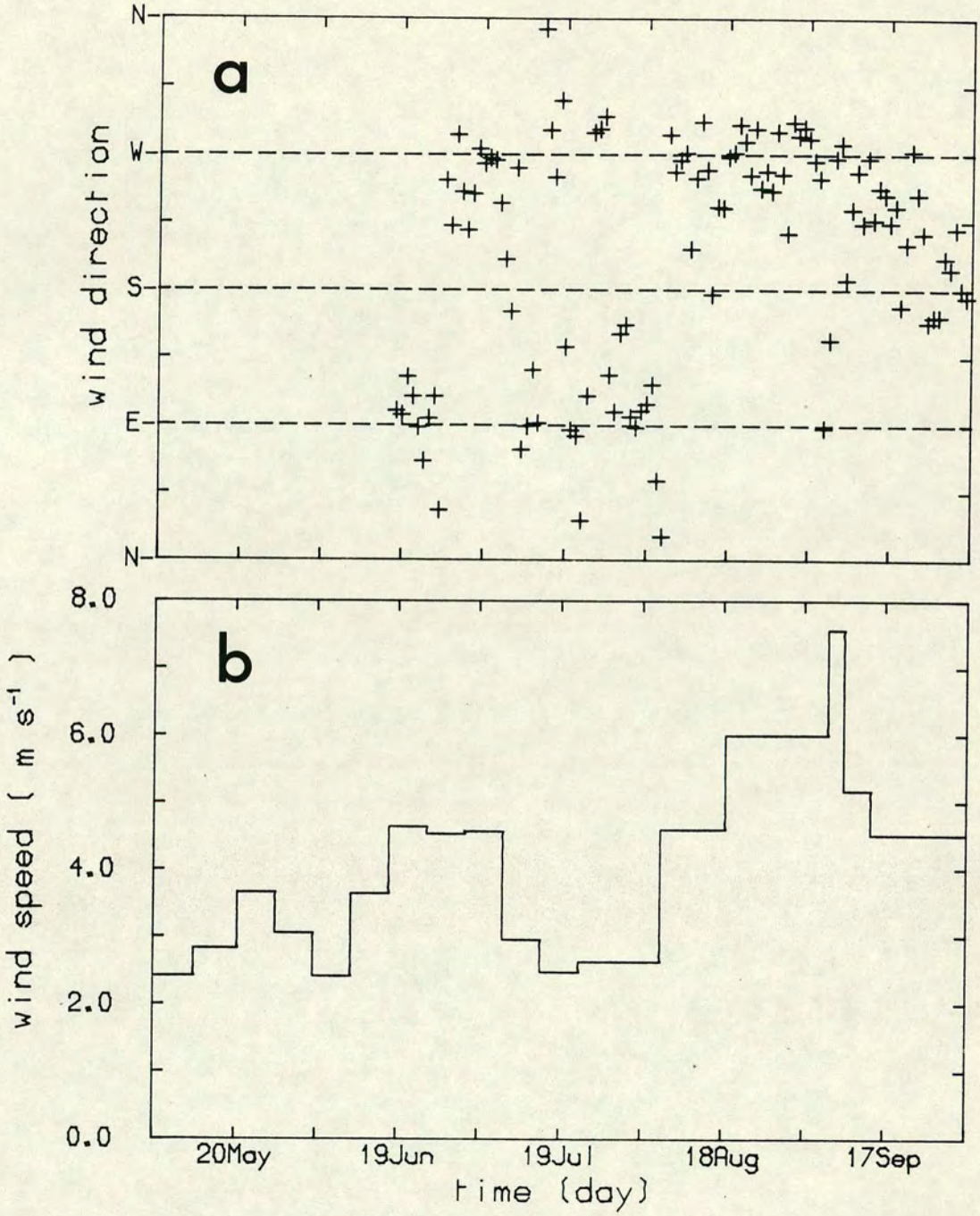


Figure 2.4. Diagram showing windspeed and direction data collected at Dunslair Heights during the summer of 1982.

(a) Wind direction: each point represents the mean wind direction for one day (direction measurements not starting until 18 June).

(b) Wind speed: Histogram showing mean wind speeds between visits to the site.

Table 2.5

Counts of terminal shoots in 1980 and 1981 whorls broken during various periods from May 1981 to June 1985; data from 15 trees; 'summer' is May-September, 'winter' is October-April.

		Number of shoots broken					
Whorl	May 1981 Number of shoots	Summer 1981	Winter 81-82	Summer 1982	Winter 82-83	May 1983 - June 1985	June 1985 Number of shoots
1980	84	3	1	5	0	37	38
1981	83	3	0	5	0	28	47
Totals	167	6	1	10	0	65	85
%	100	3.6	0.6	6.0	0	38.9	50.9

2.3.2. Needle loss by mutual abrasion

The results of the measurements, made in 1982, of damage by mutual abrasion between shoots are shown in table 2.6. The cumulative damage score (determined according to the scale described in section 2.2) for the terminal and sub-terminal shoots in each quadrant of the 1980 and 1981 whorls are given for various times during the growing season.

Damage by mutual abrasion was first observed on 24 June, and became more prevalent as the season passed. The increase in the cumulative damage score resulted from both an increase in the severity of damage exhibited by shoots already affected, and the occurrence of new damage to shoots that had been previously unharmed. Most damage occurred in quadrant 3, where by 14 September the mean score per shoot was 0.12. The mean scores for the other quadrants were 0.10 for quadrant 1, and 0.07 for quadrants 2 and 4.

The first stage of damage by mutual abrasion is needle breakage at the point where two shoots rub together when they are moved by the wind. Soon after, the broken needles turn brown and are eventually lost (see plate 2.1). By the end of the season the axes of some shoots are naked of needles for part of their length, and show signs of surface damage. In extreme cases, the axis is weakened to such a degree that the shoot breaks at the point of damage.

2.3.3. Wind-induced bending

Figure 2.5 shows the results of the field measurements of branch curvature, plotted graphically (data for 1980 whorls shown in graph (a) and for 1981 whorls shown in graph (b)). Each graph is a scatter diagram, every point representing the data for one branch, plotted on the following axes. The horizontal axis is the angle at which the branch originated (in 1981) with respect to the prevailing wind direction, so branches that initially pointed directly into the prevailing wind have an angle of 0° and those facing in the opposite direction (i.e the most sheltered branches) have an angle of 180°. The vertical axis is the angle of permanent curvature away from the prevailing wind direction that had been induced by the wind in the period 1981 to 1985. A linear regression has been fitted through the scatter of points on each graph, to show the general trend in the data.

Examination of the two graphs in figure 2.5 show that the general

Table 2.6

Cumulative scores for mutual abrasion damage to terminal and sub-terminal shoots in 1980 and 1981 whorl quadrants, determined on various days during 1982; data from 15 trees. Shoots were scored on the following scale:

Needles lost or damaged (<10%) = 1
10% to 25% of needles lost or damaged = 2
25% to 50% of needles lost or damaged = 3

		Cumulative damage score							
Quadrant number	Number of shoots	May 12	Jun 3	Jun 17	Jun 24	Jul 1	Jul 8	Jul 15	Sep 14
1	129	0	0	0	2	2	3	6	13
2	184	0	0	0	3	7	10	12	12
3	207	0	0	0	3	9	17	21	25
4	176	0	0	0	2	4	9	11	13

Plate 2.1. Damage to distal regions of branches by collision.

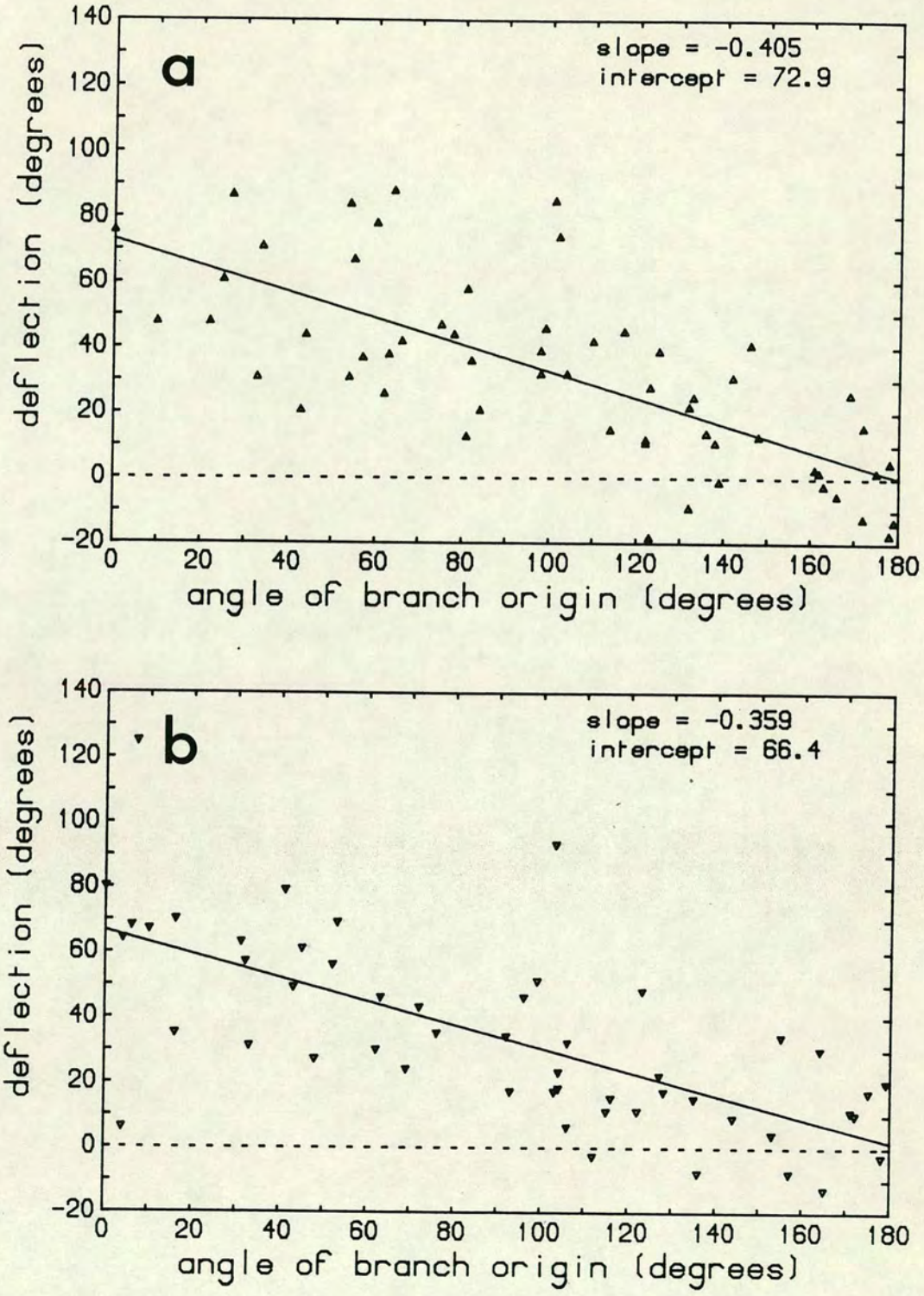


Figure 2.5. The deflection of branches away from the prevailing wind, plotted against their angle of origin, where 0° denotes pointing into the prevailing wind direction and 180° denotes pointing away from the prevailing wind direction. The upper graph (a) is for branches formed in 1980, the lower graph (b) is for branches formed in 1981, deflections being measured in 1985.

behaviour of the branches in each whorl is similar. Both regressions show an inverse relationship between the angle of branch origin and the degree of curvature induced by the wind. The branches close to the prevailing wind direction are the most bent, and the sheltered branches show little or no curvature. The slope of the regression for the 1980 whorl is slightly steeper than that for the 1981 whorl, and the intercept is also greater. Thus the branches of the 1980 whorl show, on average, more bending than those of the 1981 whorl.

2.3.4. Some field and wind-tunnel observations of shoot aerodynamics

On one occasion (18 August 1982), the field site was visited during a gale (the cup anemometer recorded a mean wind speed of 10.1 m s^{-1}), so it was possible to observe the mechanics of shoot breakage at first hand.

To aid the description of the process of shoot breakage, two schematic diagrams are presented in figure 2.6. Diagram (a) shows the top of a tree at rest, and diagram (b) shows the configuration adopted by the same structure when a strong wind is blowing. The stem bends away from the wind, and most of the branches are swept back horizontally, as a result of the drag forces experienced by the foliage. The branches which, in still conditions, point towards the direction of the wind bend upwards, in a vertical plane, until they are appressed to the stem. These exposed branches are thus bent through a much greater angle (shown by 'A' on figure 2.6b) than the other branches, which tend to bend in a horizontal plane, and so they are much more susceptible to breakage. Maximum flexion of the exposed branches occurs close to their proximal ends, where they originate from the stem. Whenever broken shoots were observed, the point of breakage was almost always close to the shoot base.

Plates 2.2 and 2.3 were taken soon after a storm and show the results of the process described above. Plate 2.2 is a close-up photograph of a whorl showing three shoots (arrowed) which were pointing towards the wind. Although they escaped breakage, they experienced so much bending that they remained in a vertical orientation. Plate 2.3 is a similar photograph, showing a tree viewed from the side that was exposed to a storm. Many shoots show the pale colour of the abaxial surfaces of their needles; some are broken, and others have escaped breakage, but remained in a vertical position.

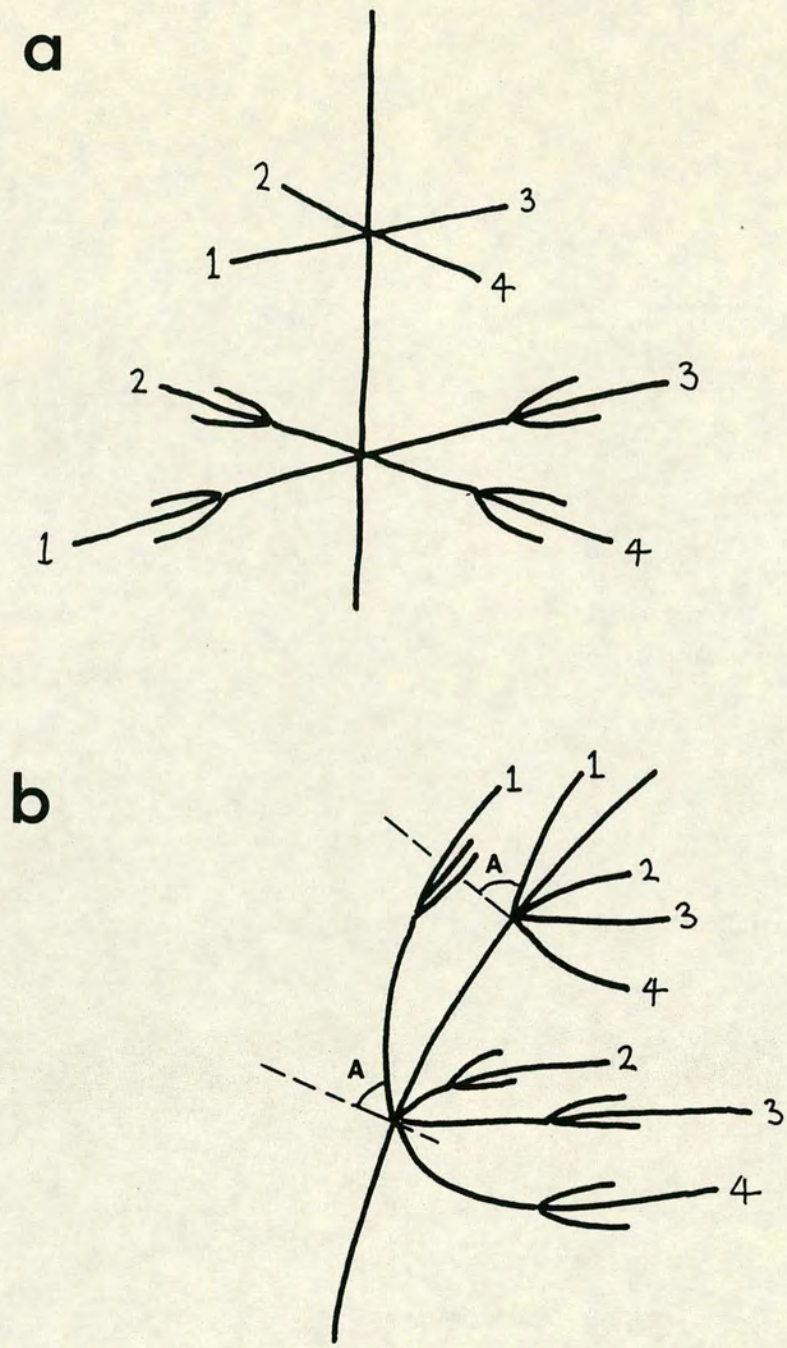


Figure 2.6. Deflections of tree-tops in strong wind. When the wind is blowing from the left so that branches labelled 1 are the most exposed, these branches deflect in a vertical plane. To be compared with Plate 2.4.

Plate 2.2. Shoots (arrowed) which have previously been deflected vertically in a strong wind remaining vertical when the wind has ceased.

Plate 2.3. Overall view of canopy after a storm. Many shoots remain in a vertical postion, exposing the bluish abaxial surface.

To support the above field observations, a potted Sitka spruce was subjected to a range of wind speeds in a wind tunnel. The resulting series of photographs is shown in plate 2.4. Each photograph shows the configuration of the tree's branches (viewed from above), the branch facing directly into the wind being marked with a white arrow. As the wind speed was increased, the deflection of the stem increased, and those branches perpendicular to the wind became ever more swept back in the horizontal plane. The arrowed shoot, however, became increasingly bent in the vertical plane, so that at higher wind speeds the pale colour of the abaxial surfaces of the needles was visible. At the highest wind speed of 12 m s^{-1} it was clearly the arrowed shoot that was experiencing the greatest degree of bending.

2.4. Discussion

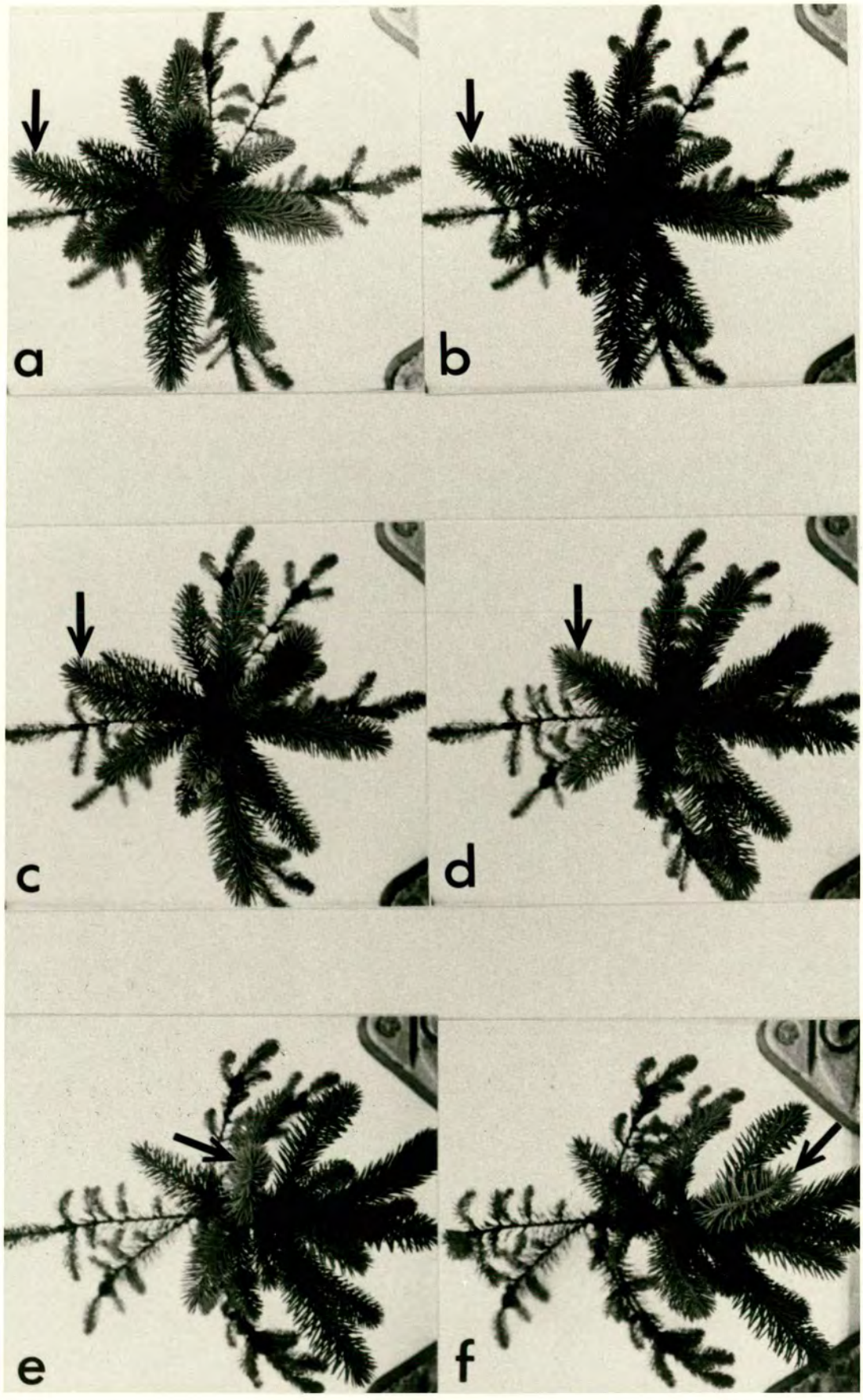
The investigation of shoot breakage during 1981 found that the most shoots were lost from the quadrant (1) facing the prevailing wind, and a neighbouring quadrant (4). Clearly, if this pattern of shoot loss were repeated, year after year, few branches would survive on the windward side of the tree, thus giving it the asymmetrical form typical of wind deformation.

The actual number of shoots broken was rather less than might be expected. It could, perhaps, have been a summer when wind speeds were generally less than average. Nevertheless, it should be noted that the loss of a single terminal shoot represents the loss of the potential to form a branch bearing a whole horizontal sector of foliage in the future crown. Even if only a small proportion of the terminal shoots are lost, all tending to face the same direction, then the crown shape of the tree would be significantly asymmetric.

During the growing season of 1982, the pattern of shoot loss was different. Most of the breakages occurred in the 'sheltered' quadrant (3), opposite the prevailing wind direction. The wind data show that these breakages occurred at a time of strong easterly winds. This confirms the idea that it is the shoots facing directly into a gale that are broken, while those with different orientations are not harmed.

It must be assumed, from the measurements of the direction of maximum crown asymmetry, that strong winds from the east are a rare event at the site, an event that chanced to occur during the period of observation. This is

Plate 2.4. Wind tunnel photographs showing the vertical deflection of a windward shoot (arrowed) as windspeed was increased from calm (a) to 12 m s^{-1} (f).


a
b
c
d
e
f

supported by the measurements of wind speed and direction made during 1984 (figure 2.3), when no wind from the east had a speed greater than 4 m s^{-1}.

It is unlikely that shoot breakage occurs at a uniform rate from year to year; more probably it is violent storms, occurring infrequently, that are responsible for most of the damage. Observations over ten or more years are needed to get a fuller picture of the pattern of shoot breakage and its relationship to prevailing wind direction.

During both 1981 and 1982, no shoot loss was observed in the early part of the period of shoot extension. Again this could be coincidental, a chance occurrence of two successive years of low wind speeds in May and June. A mean wind speed of nearly 4 m s^{-1} was, however, recorded between 20 May and 27 May, and peak speeds during this period were certainly higher, leading to the expectation of at least some damage.

It is probable that the observed lack of early breakage was a result of the small size of the new shoots. Although soft and fragile when small, they do not present much resistance to the airflow, so a very strong wind is required to produce drag forces great enough to cause them to be blown off. When they have nearly attained their final lengths, but are still not fully developed, they are much more susceptible to damage. This is because they present a considerably greater surface area to the wind, and thus experience high drag forces, yet they are still mechanically weak. The time just before the completion of extension growth can thus be viewed as a critical one for wind damage. If high winds occur at this time, many shoots are lost.

Hardly any breakage was found to occur during winter. This disagrees with the observations of some other authors (Lawrence, 1939; Daubenmire, 1959; Marchand, 1980), who considered that breakage caused by the accumulation of ice glaze in the wintertime is of primary importance in the wind deformation of trees. However, they studied trees growing at sites where much more severe winter conditions are experienced. The site used for this study has a relatively mild winter climate, so the greatest damage is done during the early part of the growing season, when the new shoots are most vulnerable.

No damage by mutual abrasion between shoots was exhibited during the

first part of the period of active extension. This was probably caused by the small size of the new shoots, which were still very short and so did not frequently come into contact with others. Once the shoots were half grown, the first signs of damage by mutual abrasion were seen. The damage became progressively worse as the summer passed, because the needles were gradually worn away by the rubbing at contact points.

The most damage by mutual abrasion occurred in the sheltered quadrant (3), but only slightly lesser amounts were observed in the other quadrants. The greatest development of foliage occurs in the sheltered quadrant so there is simply more likelihood of destructive shoot contacts occurring, as the shoots are more densely packed.

The overall proportion of shoots damaged by mutual abrasion was low. This, together with the slight prevalence of abrasive damage in the sheltered quadrant, suggests that this type of damage does not play a role in asymmetrical crown production.

The measurements of wind-induced shoot curvature show that the shoots facing the prevailing wind become the most bent (away from the wind), while the leeward shoots are hardly bent at all. The magnitude of this effect, the most exposed becoming bent by about 70°, indicates a profound effect on the shape of the tree crown, especially considering the fact that the measurements only span a period of four years. The wind-induced bending appears to be progressive, as the shoots of the older whorl were more curved than those of the younger whorl. This process clearly contributes to asymmetrical crown development shown by trees in windy places.

The reported observations of the bending behaviour of shoots in high winds (both during a storm and in the wind tunnel) explain the field observation made in 1982 (see above) that breakage is highly concentrated amongst those shoots facing almost directly into a storm. These shoots tend to bend vertically, through large angles, while shoots pointing in other directions experience lesser deflections in the horizontal plane.

This difference in behaviour results from the pattern of needle distribution around the shoot axis, and the horizontally-flattened nature of the needles. These attributes of shoot morphology cause the shoot to have a greater

projected area when viewed from below, than when viewed from the side. When the tree experiences a high wind, its stem bends away from the wind, causing upward tilting of the shoot facing into the wind. Once the shoot is slightly tilted, its lower surface is exposed to the airflow, causing the shoot to flip upwards into a vertical position. In this orientation, it presents maximum surface area to the airflow, thus experiencing the highest possible drag forces and a high degree of bending, often resulting in shoot breakage. The shoots facing in other directions are not tilted into the wind by the movement of the tree's stem, and they expose less surface area to the wind, as it is incident upon their sides. As these shoots respond to drag forces, they bend horizontally, through smaller angles than the windward shoots.

The work presented in this chapter shows that mechanical damage is very important in the wind deformation of trees. It is mostly the shoots facing into the wind that are broken during high winds, so if a tree grows at a location where one wind direction is truly prevalent, it will become more or less denuded of branches on one side. The branches that do survive on the exposed side experience maximum wind-induced curvature, further enhancing the asymmetry of the tree crown.

CHAPTER 3
EXPERIMENTAL INVESTIGATION OF SHOOT BENDING

3.1. Introduction

It has been suggested (chapter 1) that the permanent bending of branches by the prevailing wind plays an important role in the deformation of tree crowns. In section 2.3.3 the results of some field measurements of the amount of curvature induced by the wind were presented. These data showed that shoots facing the prevailing wind direction exhibited a much greater amount of wind-induced curvature than the sheltered shoots and that over a period of four years, the effect was great enough to significantly alter tree shape. The experiment reported in this chapter was designed to complement these field observations, with several objectives in mind.

Firstly, to show that similar permanent curvature can be achieved solely by mechanical means, thus making it unnecessary to invoke some other wind-induced effect. Possible alternatives to a simple mechanical process are a wind-induced hormonal redistribution or a wind-induced temperature gradient across the apical growing point.

Secondly, it was considered desirable to investigate the time course of the fixation of curvature to discover at what point in their development shoots are susceptible to permanent bending by the wind. This should give an indication of the timing and minimum duration of high winds that would be required to cause permanent shoot curvature.

Thirdly, by applying artificial bending for different proportions of the time it was intended to get some idea of the frequency of high winds that would be required to cause appreciable fixation of wind-induced curvature.

3.2. Plant material

The experiment was conducted using 10 sitka spruce of Queen Charlotte Island provenance, aged five years (from seed). These were selected for their good form and vigour from a larger group that had spent the previous winter in pots (15 cm diameter, 12 cm deep), standing outdoors on gravel, in the shelter of a wall. Immediately prior to the experiment the trees were re-potted

in University of California mix D2 compost, without disturbing their root balls, into larger pots (21 cm diameter, 15 cm deep), and transferred to the un-heated greenhouse. Bud-break had occured four weeks previously and at the beginning of the experiment the young extending shoots had achieved 68% of their final extension.

3.3. Methods

On each tree five of the current year's extending lateral shoots were selected. The shoots chosen were, as nearly as possible, of equal length. A short piece of plastic-coated copper wire was carefully wrapped around the previous year's growth, close to the base of each shoot under study, and its other end formed into a hook. A bend of 90 degrees could be applied to each shoot by slipping it into the hook (see plate 3.1). At the end of the desired period of artificial bending the shoot could be easily released by slipping it out of the hook. The processes of hooking up and releasing the shoots caused no visible damage. The following five treatments were applied to the shoots, each chosen shoot of a particular tree receiving a different treatment to its fellows:

1. Shoot bent permanently.
2. Shoot bent for 24 hours in every 48 hours.
3. Shoot bent for 8 hours in every 24 hours.
4. Shoot bent for 24 hours in every 72 hours.
5. Shoot unbent (control)

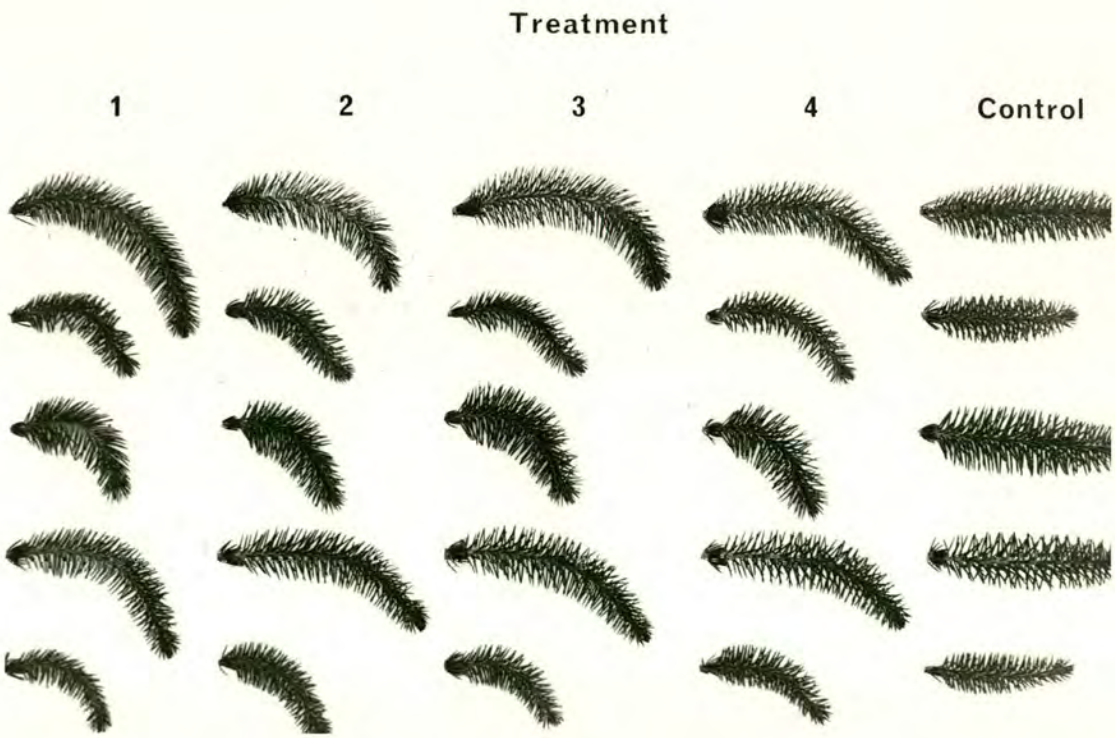
The length of the shoots and the degree of fixation of curvature was measured at intervals through the experiment. The degree of fixation was determined by using a protractor to measure the angle of curvature (see fig. 3.1) of each shoot 30 minutes after it had been released from the hook.

3.4. Results

At the start of the experiment the mean length achieved by the shoots was 68% of their final extension. At this stage of their development they were extremely floppy, dangling downwards under their own weight. They could be

Plate 3.1. Shoot of *Picea sitchensis* held in bent position by bent wire hook.

Plate 3.2. Curvature of shoots removed at the end of the bending experiment.


Treatment
1
2
3
4
Control

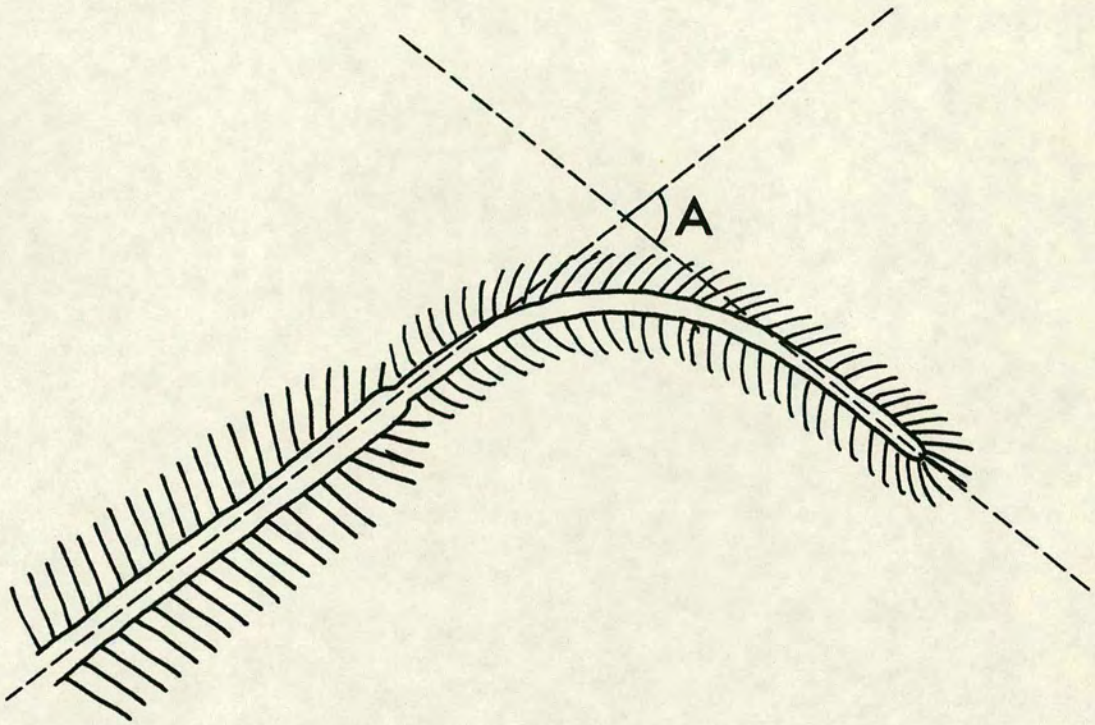


Figure 3.1. Diagram defining the angle measured in the bending experiment.

easily bent in any direction with minimal force and would instantly return to their natural, undeformed position when the force was no longer applied. As time progressed the shoots became stiffer and ~~more~~ less pliant. They ceased to hang downwards and no longer sprang back to being straight when the imposed bending force was released.

Figure 3.2 shows the degree of curvature fixed in the shoots, for each of the five treatments, plotted against time. The graph shows that for all treatments, except the control, a large proportion of the applied curvature was fixed during the first 18 days of the experiment. At this time the shoots had almost completed their extension growth (the mean length was 98% of mean final extension). During the remainder of the period when the bending treatments were applied little further curvature became fixed.

Treatment 1, where the shoots were held permanently, produced the greatest degree of bending. Here the shoots retained almost all of the applied bend of 90°. Treatments 2–4, where shoots were bent intermittently, resulted in the fixation of significantly less curvature (62°–75°). No curvature resulted from the control treatment.

Figure 3.3 shows the degree of bending achieved on 13 July, the last day of the bending treatments, plotted against the percentage of the time that bending was applied. At this time the treated shoots were removed from five of the trees and photographed (see plate 3.2). The treated shoots of the remaining trees were measured on 3 November 1982 to see how much of the curvature had been retained after the elapse of nearly five months after the cessation of the experimental treatments. These data are plotted as a second line on figure 3.3. Varying amounts of curvature had been lost by the shoots in each treatment during this period, but all the shoots retained approximately two-thirds of the curvature observed on 13 July.

The five treatments applied had no significant effect on the final lengths achieved by the shoots.

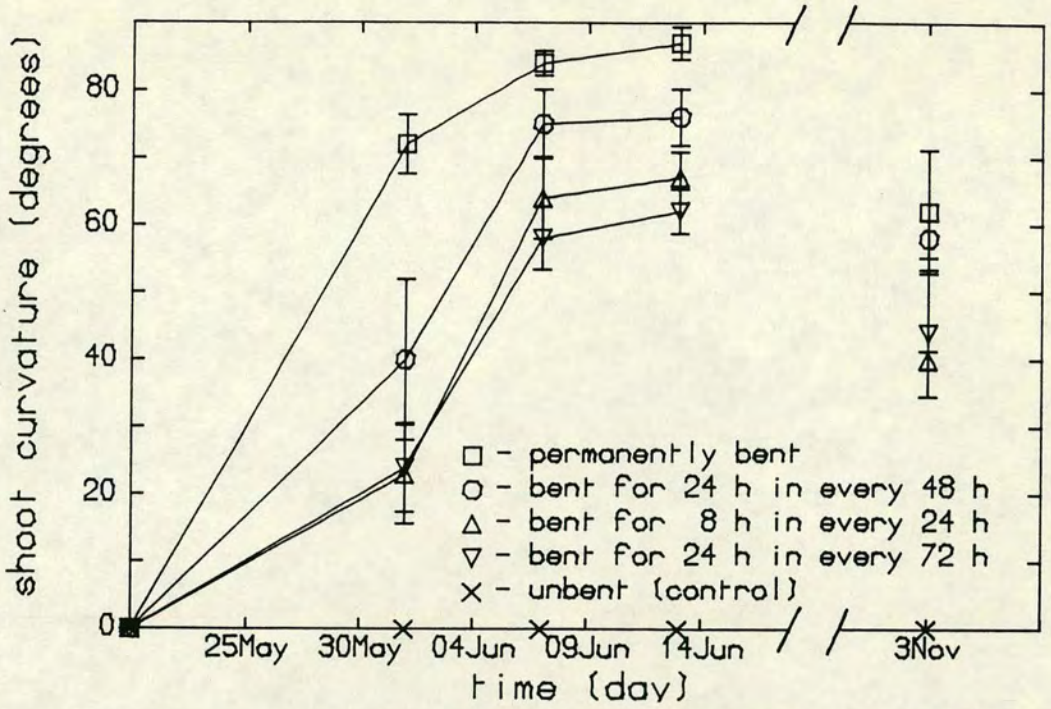


Figure 3.2. The curvature remaining after each shoot was removed from its hook.

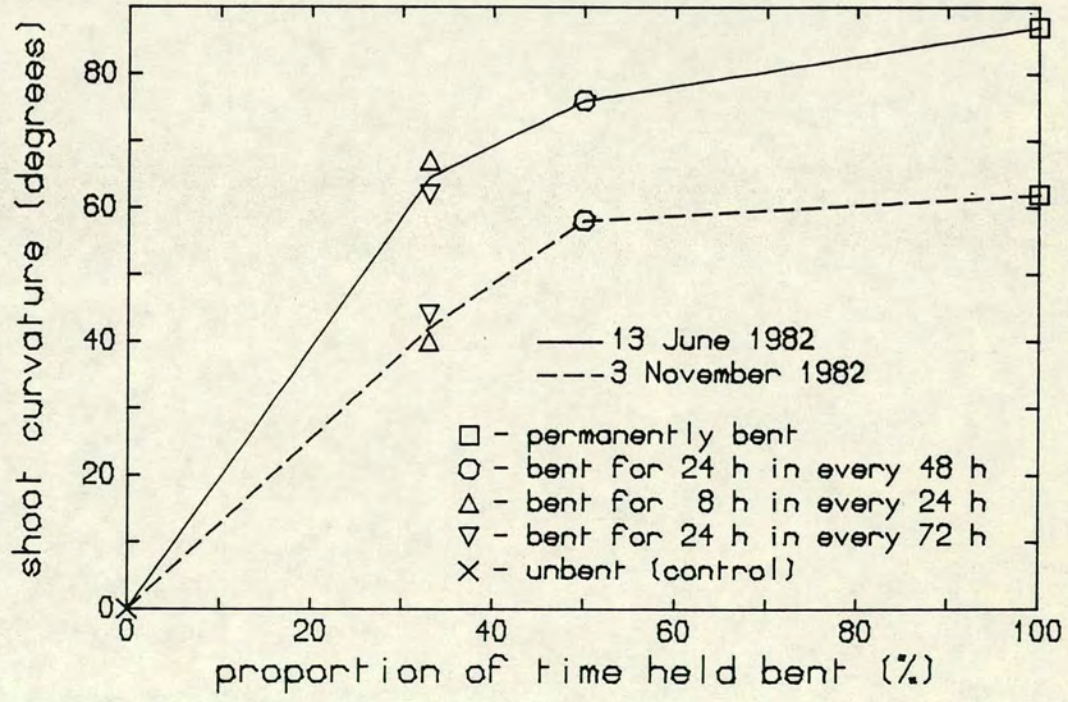


Figure 3.3. The curvature remaining after each shoot was removed from its hook, as affected by the proportion of time that the shoot had been held bent.

3.5. Discussion

The fixation of curvature occurred over a short period of time, maximum curvature occurring at about the time shoot extension ceased. It is probably at this time that lignification of the xylem occurs and rapid radial growth begins.

Even the lowest intensity bending treatment (4) produced a fair degree of permanent curvature, implying that much lower intensity bending could produce appreciably curved shoots. This is supported by, the shape of the curves in figure 3.3. Each has a steep slope initially, which declines rapidly, until a plateau is reached. These results of the experiment suggest that it is not necessary for high winds to blow permanently for curved shoots to be formed. This is liable to occur even if strong winds only persist for a few days during the phase of shoot extension when the fixation of curvature can occur (i.e. during active extension from 80% to full length).

It is impossible to make quantitative predictions of the strength and duration of winds required to produce permanent curvature. This is because the bending treatments applied in the experiment were a poor simulation of the bending experienced by a shoot on a windy day. In nature the shoot is not held motionlessly bent for long periods, it is only flexed for the duration of strong gusts of wind. This type of intermittent bending is difficult to simulate artificially, so a simpler and less realistic bending regime had to be used in this experiment. However, the shoot is not completely elastic and does not straighten instantaneously when there is a lull in the wind. Rather it has some plasticity and takes some time to straighten after a gust. This is particularly true towards the end of active extension growth, when shoots are seen to be rather slow to recover from deformation (requiring five to ten seconds).

Comparison of the two curves in figure 3.3 shows that a large proportion of the curvature fixed during the brief period of shoot extension is retained permanently.

CHAPTER 4
FIELD MEASUREMENTS OF SHOOT GROWTH

4.1. Introduction

The typical form (see chapter 2) of a wind-shaped tree is asymmetrical, there being more foliage to the leeward side of the stem than to the windward side. Inspection of wind-shaped conifers reveals that this is partially caused by the greater growth of the leeward branches, which are longer than the windward ones, showing noticeably greater annual length increments. The work reported in this chapter was undertaken both to quantify the annual variation in annual shoot increment, with relation to wind exposure, and to investigate in detail the dynamics of shoot extension. Consideration of the effects of temperature on shoot extension (see chapter 1) suggests that the greater length increments of the sheltered shoots might result from an earlier initiation of growth in the spring, later cessation of extension growth, and/or greater rates of elongation. This chapter reports detailed measurements of shoot extension, made over a two-year period, in an attempt to ascertain which of these alternatives is, or are, involved in the production of longer branches on the leeward side of the tree.

The asymmetrical distribution of foliage might result not only from differences in the annual increments of the leeward and windward shoots, but also from differences in the number of sub-terminal and internodal shoots produced by each terminal shoot. If there is a tendency for the sheltered shoots to form more buds at the end of the growing season than the exposed shoots, this would result in the production of a greater bulk of foliage on the leeward side of the tree. To investigate this possibility, the number of buds produced by each of the terminal shoots in the sample used for the extension measurements was determined for 1982 and 1984.

4.2. Methods

The measurements of shoot extension were made concurrently (during 1981 and 1982) with the measurements of shoot breakage, previously presented in chapter 2. Exactly the same shoots were studied in the 1980 and

1981 whorls of a group of Sitka spruce at Dunslair Heights, Scotland (see chapter 2 for a full description of the field site and the sample of shoots studied). The site was visited regularly through the growing seasons of 1981 and 1982. On each visit, the lengths of all the current year's branch terminal shoots in the sample were measured to the nearest millimetre with a ruler.

A final visit to the site was made in June 1985. On this occasion, the final extensions achieved by the terminal shoots in 1984 were recorded.

The mean length of the terminal shoots in each whorl quadrant (defined in section 2.3) on each visit to the site was calculated, so that the extension achieved could be related to the degree of wind exposure experienced by the shoots. An analysis of variance (single classification) using the computer package 'PRESTO' (see appendix II), was performed for each set of measurements, allowing the significance of the differences between whorl quadrants to be assessed.

In addition, relative growth rates (on a length per length basis) were determined for each of the intervals between measurements. Each set of relative growth rates was subjected to an analysis of variance (as above), to investigate the significance of the differences observed between whorl quadrants.

The production of buds by the terminal shoots in 1982 was determined (in early 1983) by counting the number of buds formed on each shoot axis. The buds were counted in three categories, terminal (1 or 0), sub-terminal, or internodal.

Bud production during 1984 was also determined. The number of new shoots (1985) originating from each of the terminal shoots (those that had not been broken off since the start of measurements in 1981) was counted in June 1985. Care was taken not to miss the remnants of any of the new shoots that had already been broken off by the wind, since bud break.

The mean production of buds of each type was determined for each of the whorl quadrants (defined in section 2.3), allowing bud production by the shoots to be related to wind exposure. Analyses of variance (single classification) were calculated, using the computer package 'PRESTO' (appendix

II), to assess the significance of observed differences between quadrants.

4.3. Results

The mean lengths of the terminal shoots in the 1980 whorl quadrants, measured on various days during the 1981 growing season are given in table 4.1 and plotted in figure 4.1a. The results of the analysis of variance are given in table 4.2.

The shoots of the most sheltered quadrant (3) and one of its neighbours (4) achieved significantly greater final extensions than the other quadrants, by a margin of approximately 9%. A significant difference in length was observed when the first measurements were made on 25 May. At this time the scales covering most of the buds had just ruptured, and those of the exposed quadrant where shortest in length, while those of the sheltered quadrant were longest (27% longer than the exposed shoots). The relative growth rates (table 4.3) of the exposed shoots were quite often greater than the sheltered shoots. From 1 July to 14 July and 30 July to 17 August the growth rate of the exposed shoots was significantly greater (table 4.4) than those of any other quadrant, but the difference was not large enough to make up for their small size at the beginning of the season.

Table 4.5 gives the mean extensions of the shoots of the different quadrants of the 1981 whorl at various times during 1981 (i.e. the whorl's first year of growth). These data are plotted in figure 4.1b. Table 4.6 gives the results of the analyses of variance.

No significant differences between the mean extensions of the shoots in the various quadrants were observed at any time, although the mean final length of the sheltered shoots (quadrant 3) was 9% greater than that of the exposed shoots (quadrant 1). At the beginning of the growing season the sheltered shoots were marginally larger than the others, but the difference was not significant. There were no significant differences in the mean relative extension rates in the 1981 whorl quadrants (tables 4.7 and 4.8).

The means calculated from the 1982 measurements of extension of the 1980 whorl are given in table 4.9 and plotted in figure 4.2a. On May 12, when the first measurements were made, bud break had not occurred. The buds of

Table 4.1

Mean lengths of terminal shoots in 1980 whorl quadrants, measured on various days during 1981; data from 17 trees.

	Mean terminal shoot length (mm)							
Quadrant number	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1	15.9	24.5	33.8	47.0	76.5	118.8	131.5	134.7
2	18.4	27.7	40.0	51.6	84.7	118.0	129.7	130.4
3	20.2	31.2	41.8	57.6	93.7	130.6	141.7	143.1
4	18.7	29.4	38.1	55.1	91.5	131.2	144.6	145.5

Table 4.2

Analyses of variance of lengths of terminal shoots in 1980 whorl quadrants measured on various days during 1981; data from 17 trees.

	Probability (only given if significant)							
Quadrant comparison	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1-2								
1-3	<0.01		<0.01	<0.01	<0.001	<0.01	<0.05	
1-4	<0.05			<0.05	<0.01	<0.01	<0.05	<0.05
2-3			<0.05		<0.05	<0.01	<0.01	<0.01
2-4						<0.01	<0.01	<0.01
3-4								
Number of cases	86	64	72	93	93	93	93	93
F-value	3.54	2.74	3.86	3.27	5.26	6.08	4.93	4.43
Probability	<0.05	NS	<0.05	<0.05	<0.01	<0.001	<0.01	<0.01

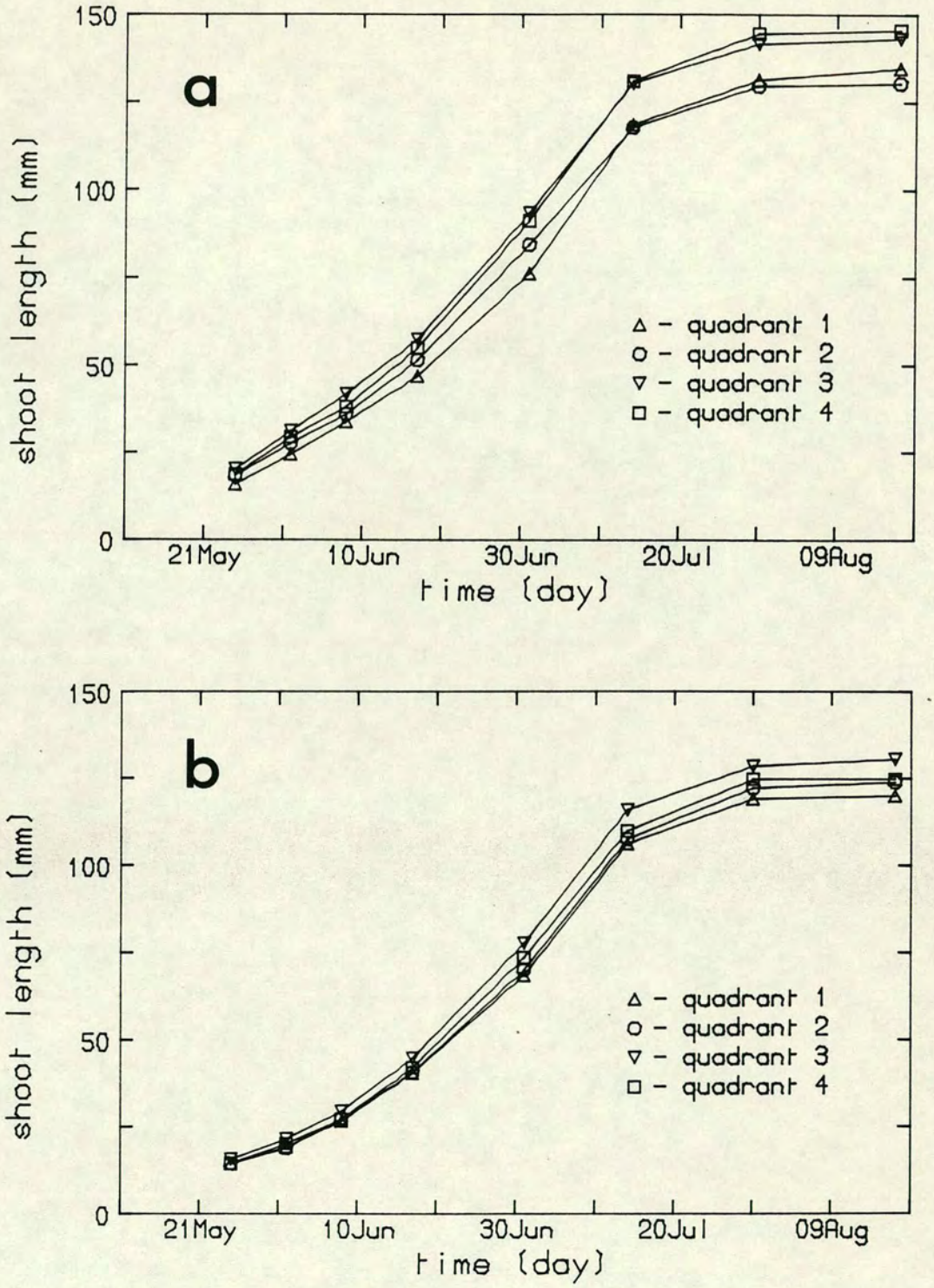


Figure 4.1. Progress in shoot length, as measured in 1981. Figure (a) is the 1980 whorl, Figure (b) is the 1981 whorl. Quadrant 3 is the most sheltered, quadrant 1 is the most exposed.

Table 4.3

Mean relative growth rates of terminal shoots in 1980 whorl quadrants, measured over various periods during 1981; data from 17 trees.

	Relative growth rates (mm cm^{-1} day^{-1})						
Quadrant number	May 25 -Jun 1	Jun 1 -Jun 8	Jun 8 -Jun 17	Jun 17 -Jul 1	Jul 1 -Jul 14	Jul 14 -Jul 30	Jul 30 -Aug 17
1	0.566	0.535	0.338	0.353	0.341	0.070	0.014
2	0.537	0.488	0.323	0.359	0.262	0.058	0.005
3	0.564	0.537	0.312	0.350	0.262	0.050	0.006
4	0.554	0.494	0.351	0.371	0.283	0.062	0.005

Table 4.4

Analyses of variance of relative growth rates of terminal shoots in 1980 whorl quadrants, measured on various days during 1981; data from 17 trees.

	Probability (only given if significant)						
Quadrant comparisons	May 25 -Jun 1	Jun 1 -Jun 8	Jun 8 -Jun 17	Jun 17 -Jul 1	Jul 1 -Jul 14	Jul 14 -Jul 30	Jul 30 -Aug 17
1-2					<0.01		<0.01
1-3					<0.01		<0.05
1-4					<0.05		<0.01
2-3							
2-4							
3-4							
Number of cases	64	51	72	93	93	93	93
F-value	0.19	0.73	0.83	0.83	4.57	0.68	3.25
Probability	NS	NS	NS	NS	<0.01	NS	<0.05

Table 4.5

Mean lengths of terminal shoots in 1981 whorl quadrants, measured on various days during 1981; data from 17 trees.

	Mean terminal shoot length (mm)							
Quadrant number	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1	14.4	19.2	26.6	40.5	68.7	106.4	119.2	120.0
2	14.4	18.8	27.3	40.6	70.3	107.7	122.3	123.9
3	15.6	21.5	29.4	44.8	78.0	116.1	128.6	130.5
4	14.4	20.1	27.1	42.0	73.8	110.0	124.8	124.7

Table 4.6

Analyses of variance of lengths of terminal shoots in 1981 whorl quadrants measured on various days during 1981; data from 17 trees.

	Probability (only given if significant)							
Quadrant comparisons	May 25	Jun 1	Jun 8	Jun 17	Jul 1	Jul 14	Jul 30	Aug 17
1-2								
1-3								
1-4								
2-3								
2-4								
3-4								
Number of cases	82	59	69	90	90	90	90	90
F-value	1.62	1.21	1.15	1.36	2.51	1.88	1.02	1.14
Probability	NS	NS	NS	NS	NS	NS	NS	NS

Table 4.7

Mean relative growth rates of terminal shoots in 1981 whorl quadrants, measured over various periods during 1981; data from 17 trees.

	Relative growth rates (mm cm^{-1} day^{-1})						
Quadrant number	May 25 -Jun 1	Jun 1 -Jun 8	Jun 8 -Jun 17	Jun 17 -Jul 1	Jul 1 -Jul 14	Jul 14 -Jul 30	Jul 30 -Aug 17
1	0.379	0.651	0.428	0.382	0.342	0.072	0.006
2	0.371	0.636	0.382	0.397	0.333	0.079	0.008
3	0.421	0.676	0.409	0.400	0.308	0.063	0.008
4	0.431	0.623	0.428	0.404	0.314	0.077	0.004

Table 4.8

Analyses of variance of relative growth rates of terminal shoots in 1981 whorl quadrants, measured on various days during 1981; data from 17 trees.

	Probability (only given if significant)						
Quadrant comparisons	May 25 -Jun 1	Jun 1 -Jun 8	Jun 8 -Jun 17	Jun 17 -Jul 1	Jul 1 -Jul 14	Jul 14 -Jul 30	Jul 30 -Aug 17
1-2							
1-3							
1-4							
2-3							
2-4							
3-4							
Number of cases	59	45	69	90	90	90	90
F-value	0.20	0.10	0.67	0.95	0.82	0.38	0.80
Probability	NS	NS	NS	NS	NS	NS	NS

Table 4.9

Mean lengths of terminal shoots in 1980 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Mean terminal shoot length (mm)					
Quadrant number	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22
1	9.0	16.0	55.6	74.8	94.6	106.0
2	9.6	16.2	69.0	87.2	102.1	107.0
3	10.5	23.5	80.9	103.8	122.2	129.4
4	10.4	20.1	77.7	100.4	121.0	131.0

Table 4.10

Analyses of variance of lengths of terminal shoots in 1980 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Probability (only given if significant)					
Quadrant comparisons	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22
1-2						
1-3	<0.05	<0.001	<0.01	<0.01	<0.01	<0.05
1-4	<0.05	<0.05	<0.05	<0.01	<0.01	<0.05
2-3		<0.001		<0.05	<0.01	<0.05
2-4		<0.05			<0.01	<0.01
3-4		<0.05				
Number of cases	73	57	73	73	73	73
F-value	3.00	9.46	3.37	4.92	6.53	4.55
Probability	<0.05	<0.001	<0.05	<0.01	<0.001	<0.01

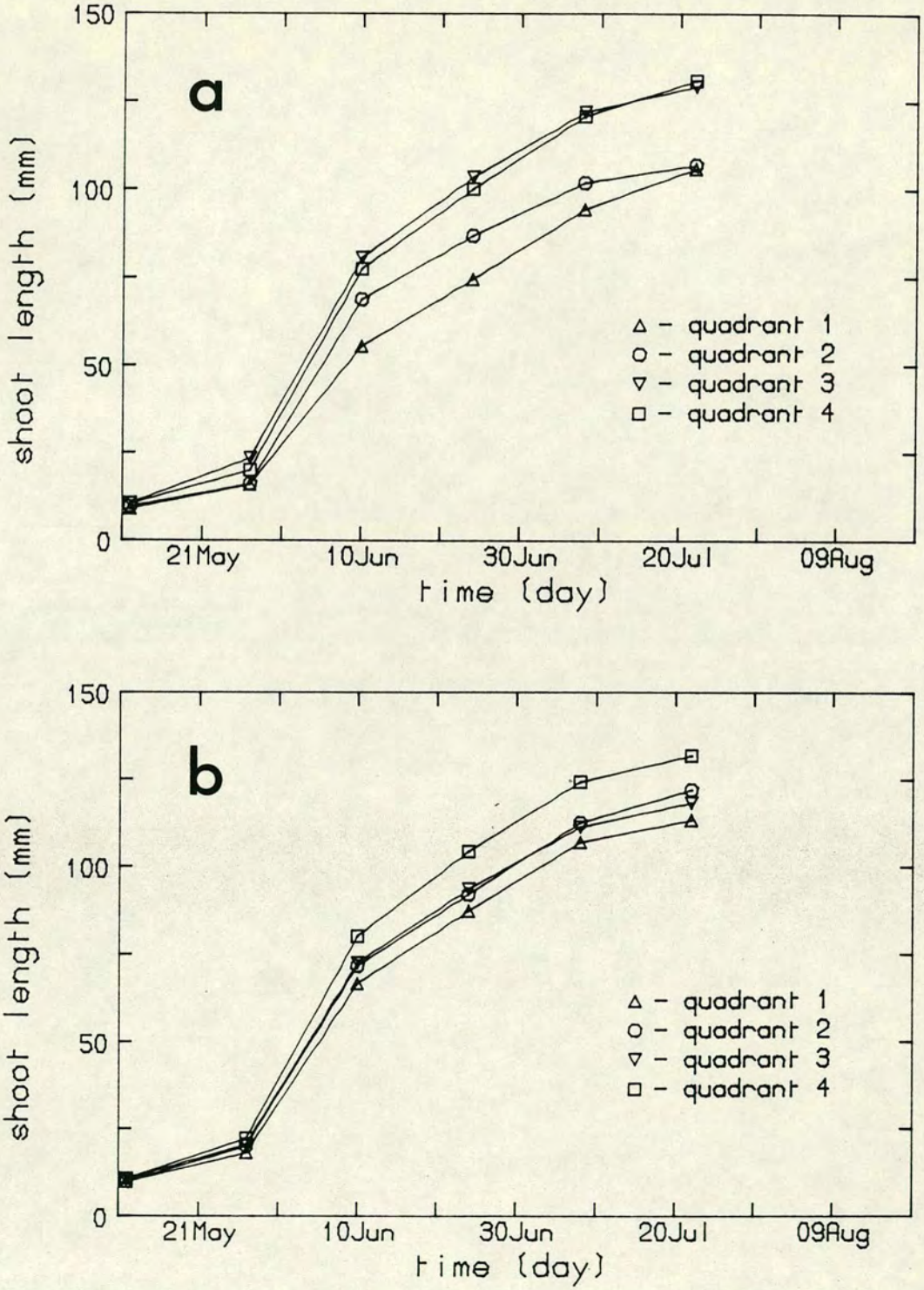


Figure 4.2. Progress in shoot length as measured in 1982. Figure (a) is the 1980 whorl, Figure (b) is the 1981 whorl. Quadrant 3 is the most sheltered, quadrant 1 is the most exposed.

the sheltered quadrant and quadrant 4 were larger than those of the exposed quadrant by a significant (table 4.10) margin of 16%. This initial superiority in length was maintained throughout the growing season, so by 22 July, the shoots of quadrants 3 and 4 were about 22% longer than those of quadrants 1 and 2.

Inspection of the calculated growth rates (table 4.11) shows that during the first interval between measurements (12 May to 27 May) the shoots of the sheltered quadrant extended more rapidly, by a highly significant margin. During the rest of the period of extension, no significant differences in growth rate were observed, although for the latter half the exposed quadrant's shoots showed the greatest extension rates.

The mean lengths of the terminal shoots in the 1981 whorl quadrants through the growing season of 1982 are given in table 4.13 and plotted in figure 4.2b. No significant differences between the mean lengths were observed at any time. The shoots of quadrant 4 had the greatest mean length throughout the period of extension, and those of the exposed quadrant (1) the least. There were also no significant differences (table 4.16) between the relative growth rates (table 4.15) of the whorl quadrants. During the early part of the period of shoot extension, quadrant 4 had the highest growth rate, but in the latter part, quadrant 1 grew fastest.

The measurements of the final extensions achieved by terminal shoots in 1984 (table 4.17) showed the greatest asymmetry in the trees' growth. The mean length of the sheltered shoots (quadrant 3) was 52% greater than that of the windward shoots (quadrant 1). This difference was highly significant (table 4.18). The mean lengths of the other quadrants were intermediate.

The measurements of bud production in 1982 (table 4.19) show some significant differences between quadrants. Quadrant 4 produced significantly more (13%) buds than quadrants 1 and 2. This difference was mainly accounted for by the increased production of internodal buds.

In 1984, the sheltered quadrant (3) produced the most buds per shoot and the exposed quadrant (1) the least, although the difference was not statistically significant. There was, however, a significant difference in the production of internodal buds, the shoots of the sheltered quadrant producing 74% more

Table 4.11

Mean relative growth rates of terminal shoots in 1980 whorl quadrants, measured over various periods during 1982; data from 15 trees.

	Relative growth rates (mm cm^{-1} day^{-1})				
Quadrant number	May 12 -May 27	May 27 -Jun 10	Jun 10 -Jun 24	Jun 24 -Jul 8	Jul 8 -Jul 22
1	0.340	0.578	0.107	0.073	0.030
2	0.383	0.547	0.087	0.051	0.014
3	0.542	0.521	0.103	0.049	0.015
4	0.414	0.580	0.094	0.059	0.022

Table 4.12

Analyses of variance of relative growth rates of terminal shoots in 1980 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Probability (only given if significant)				
Quadrant comparisons	May 12 -May 27	May 27 -Jun 10	Jun 10 -Jun 24	Jun 24 -Jul 8	Jul 8 -Jul 22
1-2					
1-3	<0.001				
1-4					
2-3	<0.001				
2-4					
3-4	<0.01				
Number of cases	57	57	73	73	73
F-value	8.46	1.30	0.35	1.56	1.11
Probability	<0.001	NS	NS	NS	NS

Table 4.13

Mean lengths of terminal shoots in 1981 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Mean terminal shoot length (mm)					
Quadrant number	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22
1	9.8	18.2	66.8	87.6	107.2	113.5
2	9.8	20.1	71.9	92.4	112.8	122.1
3	10.5	20.6	72.8	93.9	111.5	118.4
4	10.7	22.3	80.4	104.6	124.5	131.9

Table 4.14

Analyses of variance of lengths of terminal shoots in 1981 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Probability (only given if significant)					
Quadrant comparisons	May 12	May 27	Jun 10	Jun 24	Jul 8	Jul 22
1-2						
1-3						
1-4						
2-3						
2-4						
3-4						
Number of cases	72	59	72	72	72	72
F-value	2.25	2.54	1.43	1.98	2.24	1.92
Probability	NS	NS	NS	NS	NS	NS

Table 4.15

Mean relative growth rates of terminal shoots in 1981 whorl quadrants, measured over various periods during 1982; data from 15 trees.

	Relative growth rates (mm cm^{-1} day^{-1})				
Quadrant number	May 12 -May 27	May 27 -Jun 10	Jun 10 -Jun 24	Jun 24 -Jul 8	Jul 8 -Jul 22
1	0.401	0.567	0.099	0.062	0.017
2	0.458	0.569	0.088	0.061	0.023
3	0.438	0.517	0.087	0.049	0.016
4	0.482	0.571	0.094	0.054	0.017

Table 4.16

Analyses of variance of relative growth rates of terminal shoots in 1981 whorl quadrants, measured on various days during 1982; data from 15 trees.

	Probability (only given if significant)				
Quadrant comparisons	May 12 -May 27	May 27 -Jun 10	Jun 10 -Jun 24	Jun 24 -Jul 8	Jul 8 -Jul 22
1-2					
1-3					
1-4					
2-3					
2-4					
3-4					
Number of cases	59	59	72	72	72
F-value	1.21	1.13	0.57	0.65	0.34
Probability	NS	NS	NS	NS	NS

Table 4.17

Mean final length achieved by terminal shoots in 1980 and 1981 whorl quadrants during the 1984 growing season (measurements made on 8 June 1985; data from 15 trees).

Quadrant number	Mean final shoot length (mm)
1	128.1
2	171.1
3	195.0
4	166.0

Table 4.18

Analysis of variance of final shoot lengths achieved by terminal shoots in 1980 and 1981 whorl quadrants during the 1984 growing season (measurements made on 8 June 1985; data from 15 trees).

Quadrant comparisons	Probability
1-2	<0.05
1-3	<0.001
1-4	NS
2-3	NS
2-4	NS
3-4	NS
Number of cases	77
F-value	4.31
Probability	<0.01

Table 4.19

Mean number of buds produced per terminal shoot in each quadrant of 1980 and 1981 whorls (measurements made on 19 May 1983; data from 15 trees).

	Mean number of buds produced by each terminal shoot		
Quadrant number	Sub-terminal buds	Internodal buds	Total buds
1	3.2	3.8	7.9
2	3.3	3.5	7.8
3	3.5	4.0	8.5
4	3.4	4.5	8.9

Table 4.20

Analyses of variance of number of buds produced per terminal shoot in each quadrant of 1980 and 1981 whorls (measurements made on 19 May 1983; data from 15 trees).

	Probability (only given if significant)		
Quadrant comparisons	Sub-terminal buds	Internodal buds	Total buds
1-2			
1-3			
1-4		<0.05	<0.05
2-3			
2-4		<0.01	<0.01
3-4			
Number of cases	144	144	144
F-value	1.32	3.17	2.94
Probability	NS	<0.05	<0.05

Table 4.21

Mean number of buds produced per terminal shoot in each quadrant of 1980 and 1981 whorls (measurements made on 8 June 1985; data from 15 trees).

	Mean number of buds produced by each terminal shoot		
Quadrant number	Sub-terminal buds	Internodal buds	Total buds
1	4.0	4.6	9.5
2	4.8	7.1	12.9
3	4.8	8.0	13.6
4	4.7	6.3	12.0

Table 4.22

Analyses of variance of number of buds produced per terminal shoot in each quadrant of 1980 and 1981 whorls (measurements made on 8 June; data from 15 trees).

	Probability (only given if significant)		
Quadrant comparisons	Sub-terminal buds	Internodal buds	Total buds
1-2		<0.05	
1-3		<0.01	
1-4			
2-3			
2-4			
3-4			
Number of cases	77	77	77
F-value	0.66	3.60	2.70
Probability	NS	<0.05	NS

than those of the quadrant facing the prevailing wind direction.

4.4. Discussion

The results of the extension measurements clearly show that the trees grew asymmetrically with respect to the prevailing wind direction. The more sheltered branches achieved significantly greater annual length increments than the more exposed ones on the windward side of the tree.

The degree of asymmetry appears to increase as a whorl becomes older. After the first year of growth, whorl asymmetry was not statistically significant (1981 whorl, during 1981). At the end of the second year of growth, whorl asymmetry was 9% (1980 whorl, during 1981). For a three year old whorl (1980 whorl, during 1982), an asymmetry of 22% was measured. The oldest whorls examined, aged four and five years (1981 and 1980 whorls, during 1984), showed the greatest asymmetry of 52%.

The detailed measurements of extension made in 1981 and 1982 provide some information on the way in which the differences in the final extensions of the sheltered and exposed shoots arose. Inspection of the form of the relationships between extension and time (figures 4.1 and 4.2) shows that the growth of the shoots in the four quadrants was closely synchronised i.e. there was no apparent difference in the timing of the initiation or cessation of extension growth. Much more important were differences in relative growth rates and the initial sizes of buds.

At the beginning of the growing season, the terminal buds of the sheltered shoots were found to be longer than those of the exposed shoots. During the initial phase of shoot growth, the sheltered shoots extended more rapidly than the exposed ones (particularly in the oldest whorl studied). Later, when growth rates were generally lower, the situation was reversed, the exposed shoots tending to show greater extension rates.

A tentative explanation of this pattern of shoot growth can be constructed from a consideration of the interaction between the distribution of temperature over the tree crown and the deterministic nature of shoot growth in Sitka spruce.

Theoretical calculations (section 5.1.1) show that under some

circumstances, the apices of the leeward, sheltered shoots would be expected to be warmer than those of the exposed shoots. Sizeable temperature differences have been found to occur across trees in their natural environment (chapters 5 and 6), for some of the time. As the growth rates of trees are known to depend primarily on temperature (see chapter 1), the observation of greater extension rates for the sheltered shoots suggests that temperature differences may play an important role in the asymmetrical growth of wind shaped trees.

As a whorl ages, its dimensions and the leaf area that it supports become greater, providing more shelter from the wind for the leeward shoots. The temperature advantage of the sheltered shoots would be expected to increase as the whorl ages, because of this increase in shelter. This expectation is confirmed by measurements reported in chapter 6; sheltered buds near the base of a tree were found to be substantially warmer than those close to its apex.

This observation provides a possible explanation for the greater asymmetry of growth observed for older whorls, and lends further support to the suggestion that temperature differences are primarily responsible for the asymmetrical growth of wind-deformed trees.

Once established, asymmetrical growth is likely to be enhanced, as time progresses, by the carry-over of assimilate reserves from previous years. The greater extension of the sheltered shoots in one year appears to result from the formation of larger buds at the end of the previous growing season. Their greater size indicates that their extension growth, pre-determined for the next year, exceeds that pre-determined for the smaller buds of the exposed shoots. Hence the sheltered shoots possess an initial advantage for the next year, as well as benefitting from higher temperatures during its growing season. By virtue of their greater length and leaf area, the sheltered shoots tend to produce more photosynthate, allowing them to form even larger buds at the end of the summer. Thus, as the years pass, there will be a tendency for the sheltered shoots to accrue more and more 'capital', enhancing the asymmetrical growth of the whorl as it ages.

The calculated relative extension rates show that the *exposed* shoots grew faster than the sheltered ones towards the end of the growing season. This

conflicts with the notion that asymmetrical growth results from higher temperatures experienced by the sheltered shoots. During the latter part of the summer, the sheltered shoots would still be expected to be generally warmer than the exposed ones, so if their growth rate was truly dependent on temperature, they would be expected to show the most rapid growth.

The conflict can perhaps be resolved by considering the fact that the shoot growth of Sitka spruce is largely determined by the conditions experienced during the previous growing season, when the buds were formed. The rapid early extension of the sheltered shoots causes them to achieve the majority of their pre-determined growth sooner than the cooler, exposed shoots. At this stage they extend slowly as most of their pre-determined growth capacity is exhausted. The exposed shoots grow slower initially, so that more of their pre-determined growth remains to be made in the latter part of the summer, so their growth rate exceeds that of the sheltered shoots. The measurements of bud production showed a general tendency for the more sheltered shoots to produce a greater number of buds per shoot than the more exposed shoots. The difference was largely accounted for by a much greater production of internodal buds, presumably resulting from the greater length of the leeward shoots. This tends to increase the bulk and density of foliage on the tree's sheltered side.

The greater development of foliage on the leeward side of the wind-shaped spruces thus resulted from both asymmetry in branch extensions and the production of differing numbers of buds per shoot. The differences in the annual length increments of the exposed and sheltered branches arose from differences in initial bud sizes (which were determined by the previous year's conditions) and growth rates, rather than from differences in the timing or duration of growth.

CHAPTER 5

MEASUREMENT OF BUD TEMPERATURES AT THE ALPINE TREE-LINE

5.1. Introduction

Gates (1980) has drawn attention to the large temperature differences that sometimes exist between the sheltered and exposed sides of trees and suggested that these differences could be responsible for the asymmetrical crown development typical of wind-shaped trees:

> "I have studied the temperatures of clusters of needles in Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*) at timberline in the *krummholz* stands. For full sunshine, the needles are at air temperature on the windward side of a tree and up to 9 °C above air temperature on the leeward side. I believe that the considerably greater warmth of the plant tissues on the leeward side is in part responsible for the accelerated growth of the tree on this side. All *krummholz* trees have the habit of growing downwind. This amount of temperature difference could have notable influence on their growth."

Warren Wilson (1957) also reports the existence of sizeable temperature differences (up to 5 °C) between the sides of a large clump of *Dryas integrifolia* growing in the arctic. He also investigated the effect of sheltering a leaf of *Salix arctica* with a piece of card and observed a 4 °C temperature increase in two minutes. Larcher (1980) cites the data of Pannier *et al* who measured the distribution of temperature over the surface of the giant rosette plant *Espeletia schultzii*. The highest temperature was found at the plant apex, which is sheltered by a surrounding rosette of leaves. Here the temperature was 16 °C greater than ambient.

The foregoing observations suggest that the leeward side of a plant, which is sheltered by the plant's own foliage, will for some of the time be substantially warmer than the windward side. A two-week trip to the Austrian Tyrol provided an opportunity to make some preliminary field measurements of the distribution of temperature amongst the foliage of trees growing in windy areas close to the altitudinal limit of tree growth in the Alps. The intention was to investigate the magnitude of the temperature difference between the

windward and leeward sides of a conifer species and its relationship to the magnitudes of other microclimatic variables.

It was decided to measure the temperatures of the shoot apices, rather than the needles. This decision was dictated by several considerations. The shoot apex is liable to experience larger excess temperatures above air than the needles, because of the effect of its larger size on the rate of heat loss by convection (see section 5.1.1 for further details). So the most extreme differences between the temperatures of the exposed and sheltered sides of a tree should be found if apical temperatures are measured. Moreover, there are good physiological reasons for choosing to measure apical temperature.

The temperature sensitivity of active shoot extension results from the effect of temperature on the rates of cell division and expansion occurring in the apical meristems (Kozlowski, 1971). Warmth increases the rates of these processes and thus promotes more rapid growth. It also affects the rate of production of stimulatory growth substances (Kozlowski, 1971). Outwith the period of summer growth, resting buds are present at the shoot apices (this was the case during the mesurements reported in this chapter). The temperatures experienced by buds, when they are developing in the latter part of the growing season, controls the amount of predetermined shoot growth that occurs in the next summer. Bud temperature is also of key importance in determining the time at which active shoot growth commences.

A major constraint was imposed on the investigation by the transportation of equipment. All the necessary instruments had to be carried as hand-luggage on an airliner, so it was of paramount importance that they should be lightweight and small.

In the next section the theory of the energy balance of plant parts is discussed to give an insight into the interaction of factors determining plant temperature and to show the theoretical grounds for expecting to observe a difference in temperature between parts exposed to the wind and those sheltered from it.

5.1.1. Energy balance theory

The simplest description of the energy balance of a plant part is that the net heat gained by radiative exchanges with the environment is equal to the heat lost by a variety of processes. This may be formally expressed as below:

$$R = \lambda E + C + S + G + P \qquad (5.1)$$

where **R** = net heat gained through radiative exchanges, allowing for the absorption of both downward and upward components of long and short wave radiation (W m^{-2})
λ = latent heat of vaporization (J kg^{-1})
E = evaporation rate (kg m^{-2} s^{-1})
C = heat lost by convection (W m^{-2})
S = rate at which heat is stored (W m^{-2})
G = conduction of heat to plant body (W m^{-2})
P = rate at which energy is used in photosynthesis (W m^{-2})

The terms **G** and **P** are of negligible magnitude in most cases, so are normally excluded from the analysis (Grace, 1983). The storage term, **S**, may also be dropped when considering the energy balance of small plant parts over periods of minutes (as in the present study) as its average value approximates to zero (Grace, 1983). Thus, rewriting equation 5.1:

$$R = \lambda E + C \qquad (5.2)$$

For Arolla pine buds, which are tightly covered with resinous scales, it is likely that very little water loss occurs. A similar assumption was made by Landsberg *et al* (1974) in their study of the energy balance of apple buds. Therefore, assuming $\lambda E = 0$:

$$R = C \qquad (5.3)$$

C can be expressed in terms of a driving gradient for heat loss, an opposing heat transfer resistance, and physical constants, so that:

$$R = \frac{\rho\, C_p\, (T_s - T_a)}{r_a} \qquad (5.4)$$

where ρ = density of the air (kg m^{-3})
C_p = specific heat capacity of air at constant pressure (J kg^{-1} $°C^{-1}$)
T_s = bud surface temperature (°C)
T_a = air temperature (°C)
r_a = boundary layer resistance to heat transfer (s m^{-1})

Equation 5.4 can be rearranged to show that the bud-to-air temperature differential, $(T_s - T_a)$, is directly proportional to r_a:

$$T_s - T_a = \frac{R\, r_a}{\rho\, C_p} \qquad (5.5)$$

The magnitude of r_a is dependent on wind speed. This is shown by the following expression for the resistance of the boundary layer over a flat plate in a turbulent wind (Grace, 1983):

$$r_a = \frac{d^{0.2}\ \nu^{0.25}}{0.03\ \kappa^{0.67}\ u^{0.8}} \qquad (5.6)$$

where d = dimension of plate parallel to flow (m)
ν = kinematic viscosity of air (m^2 s^{-1})
κ = thermal diffusivity of air (m^2 s^{-1})
u = wind speed (m s^{-1})

Similar expressions have been found for other simple shapes such as spheres and cylinders; appropriate indices are given in Monteith (1973). Using superscript 'ex' to denote a quantity which is an attribute of the exposed and superscript 'sh' to denote a quantity relating to a sheltered bud, then:

$$u^{ex} > u^{sh} \tag{5.7}$$

This is caused by the attenuation of the wind as it passes through a tree crown. An exposed bud, on the windward side of the tree, is surrounded by air flowing at a speed close to that of the ambient wind. A sheltered bud, on the leeward side of the tree, is protected from the wind by the tree's foliage, so the air flowing over it moves at a speed which is markedly less than that of the ambient wind.

Assuming relationship 5.7, inspection of equation 5.6 indicates that:

$$r_a^{ex} < r_a^{sh} \tag{5.8}$$

Rewriting equation 5.5 explicitly for an exposed and a sheltered bud:

$$(T_s^{ex} - T_a) = \frac{R^{ex}\, r_a^{ex}}{\rho\, C_p} \tag{5.9}$$

$$(T_s^{sh} - T_a) = \frac{R^{sh}\, r_a^{sh}}{\rho\, C_p} \tag{5.10}$$

Bearing in mind relationship 5.8, while examining equations 5.9 and 5.10 it is clear that:

$$T_s^{ex} < T_s^{sh} \tag{5.11}$$

i.e. the temperature of a sheltered bud will be greater than that of an exposed bud if $R^{ex} \simeq R^{sh}$. Assuming $R^{ex} = R^{sh} = R$ and subtracting equation 5.9 from equation 5.10, the temperature difference, ΔT, between the sheltered and exposed buds can be expressed as follows:

$$(T_s^{sh} - T_s^{ex}) = \Delta T = \frac{R\,(r_a^{sh} - r_a^{ex})}{\rho\, C_p} \qquad (5.12)$$

From this relationship it can be seen that energy balance theory predicts a positive difference in temperature between a sheltered and an exposed bud, this difference arising from the effect of sheltering by the tree's foliage on the boundary layer resistance of the leeward bud.

Equation 5.12 rests on the assumption that the rate of water loss from the bud surface is negligible, so that $\lambda E = 0$. If this assumption is invalid, it is not simple to predict the likely effect on the magnitude of ΔT, as the rate of water loss from a plant surface is determined by the complex interplay of several factors - surface resistance to water vapour transfer, boundary layer resistance, surface-to-air vapour pressure difference and the amount of net radiation absorbed.

Grace (1981) gives a series of graphs of the relationship between boundary layer resistance and the rate of water loss, under a range of conditions. These graphs show that at high levels of net radiation (i.e. when equation 5.12 predicts that ΔT is maximal), evaporation rate increases with boundary layer resistance. Thus the expected rate of evaporation from the sheltered shoot apex will exceed the rate for the exposed shoot apex, as $r_a^{ex} < r_a^{sh}$. This will tend to reduce the temperature of the sheltered shoot apex more than that of the exposed shoot apex, so diminishing the maximum values of ΔT.

5.1.2. Description of the site of field measurements

The field site was situated on the south-west slope of Mt. Patscherkofel, at a height of 2130 m above sea-level. Mt. Patscherkofel (47° 13′ N, 11° 29′ E) lies to the south-east of Innsbruck, Austria, at a distance of 7 km (fig. 5.1 is a map of the locality).

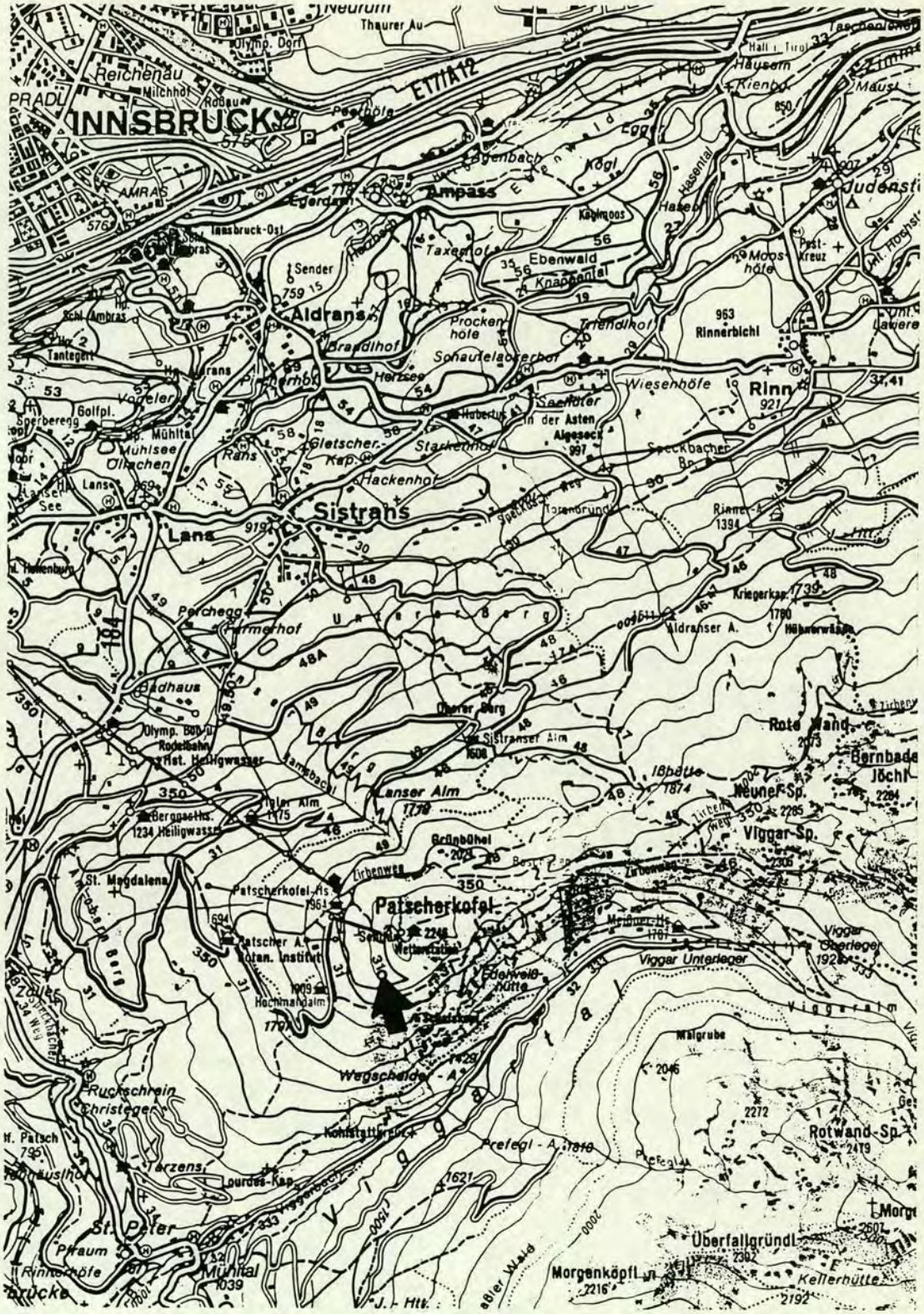


Figure 5.1. Map showing the area around Mt. Patscherkofel, Austria. The location of the field site is marked with an arrow. Scale 1:50000.

The trees used for the measurements were part of a group of Arolla pines (*Pinus cembra*) growing on an exposed, windswept ridge. The Arolla pine is one of the dominant tree species at the altitudinal limit of tree growth in the Austrian Tyrol, where it often forms almost single species stands (Tranquillini, 1979). The trees studied were of the *krummholz*-type growth form, typical of trees growing in exposed sites close to the tree-line. They were multi-stemmed and bushy in appearance, each individual being elongated in the presumed (judging from topography) prevailing wind direction. All individuals were less than 2 m tall at their highest point.

5.2. Methods

This section deals with the instrumentation used for the measurements. Each part of the system is described in detail below. Due to various logistic problems it was only possible to make satisfactory measurements on three days. On each day a different individual tree was used, but they were all of similar size and form, growing close together on an exposed ridge. Plate 5.1 shows the portable instrumentation in use, together with one of the Arolla pines selected for study.

5.2.1. Temperature measurement

The bud temperatures were measured with fine thermocouples, constructed by soldering 0.05 mm diameter copper and constantan wires. These sensors were selected for a number of reasons. Firstly, it is important that the sensor should not interfere with natural energy exchanges between the bud and its environment otherwise the 'true' temperature will not be sensed. Idle (1968) suggested that accurate measurements of leaf temperature may be obtained with thermocouples or thermistors of the smallest practicable dimensions,

> "on the grounds of interfering least with the energy and material fluxes, of not plugging up the stomata, and of avoiding the conduction of heat to or from the selected spot."

Secondly, in this investigation the primary interest is focussed on the bud-to-air temperature difference as it is this quantity that is directly dependent, via the boundary layer resistance, on the degree of sheltering. Thermocouples are the only commonly available sensors that measure

Plate 5.1. Instrument exposure at the alpine tree-line, Mt. Patscherkofel.

differential temperatures. The voltage output from a pair of thermocouple junctions gives, in a single reading, a measure of the difference in temperature between them. This feature made thermocouples a convenient choice for this study, where measurements allowing comparisons between bud-to-air temperature differences at a variety of positions in a tree crown were required.

Thirdly, several thermocouple junctions can be wired together in parallel to provide a measurement of the mean temperature difference between themselves and an additional 'reference' junction. At any particular position amongst a tree's foliage it is likely that there will be some variation in temperature between neighbouring buds, caused by slight differences in exposure to the wind and solar radiation. Thus it is desirable to know the mean temperature of a sample of buds as this will provide a more reliable basis for the comparison of bud temperature in different parts of the crown. The use of thermocouple junctions connected in a parallel configuration allows the mean temperature to be measured with a single reading, instead of measuring each bud's temperature individually and calculating the average temperature later. This permits a desirable reduction in the number of recording channels required. Miller (1971) presents criteria that can be used to select a sample size that will ensure adequate accuracy. For this study a sample size of four was chosen as a reasonable compromise between accuracy and convenience, bearing in mind that the buds of interest are situated at the extreme branch tips at the limit of the crown, so little intershading would be expected.

Lastly, an important advantage of thermocouples is that their voltage output, over the range of differential temperature likely to be encountered in this study (say -2°C to 10 °C), shows an effectively linear relationship to temperature difference. This simplifies the problem of recording the output, and allows the use of voltage integration to determine an average temperature differential over a period of time. This would not be possible with a sensor producing an output which is curvilinear with respect to temperature (e.g. a thermistor), without the use of a lineariser unit to condition the signal before integration.

The wire (Dural Plastics and Engineering, N.S.W., Australia) used to manufacture the sets of parallel junctions consisted of two 0.05 mm diameter

enamelled conductors, one of copper and one of constantan, enclosed in flexible PVC sleeving. Each junction was formed by stripping off about 5 cm of the sleeving, removing about 1 cm of enamel by passing the wires quickly through a 'cool' Bunsen flame, cleaning them with acetone, twisting and soldering. The final stage was clipping the soldered junction to the minimum size consistent with mechanical durability.

Each thermocouple set was calibrated by the following procedure. The four 'measuring' junctions were immersed in a thermostatically-controlled waterbath (Grant Instruments, Cambridge; model DP50) whose temperature was monitored with a platinum resistance thermometer (Guildline Instruments, Canada; model 9535) reading to a precision of 0.001 °C, and a long term accuracy of 0.03 °C. The single 'reference' junction was maintained at 0 °C in a thermos flask filled with a slush of crushed ice and water. The temperature difference between the measuring and reference junctions could be varied from 0 °C to 10 °C by altering the temperature of the water bath. To check if the response was symmetrical about 0 °C the junctions were simply interchanged between the ice-slush and the water-bath.

For copper-constantan thermocouples the standard Seebeck coefficient (the change in microvoltage output per Celsius degree change in temperature difference) is 38.8 μV / °C (Fritschen and Gay, 1979). The regression statistics given in table 5.1 show that for the batch of wire used for all the measurements reported in this thesis the coefficient varied from 36.1 to 36.6 μV / °C. The value obtained from each individual calibration was used when converting recorded thermocouple output voltage to a temperature reading. Calculations (Parker, 1979) based on the 95% confidence intervals for the slope and intercept of the 'worst case' calibration regression suggest that the thermocouples were able to resolve a temperature difference of 10 °C with an accuracy of ±0.1 °C.

Each 'measuring' thermocouple junction was attached to a bud by inserting it into a small hole bored with a sewing needle. This proved to be an extremely secure method of attachment, as the hole soon filled up with sticky resin. Three sets of parallel thermocouples were used to measure the average temperature of four buds on three shoots, each shoot occupying a contrasting position in the tree crown with respect to wind exposure. The 'apical' shoot

Table 5.1

Regression statistics from the calibration of four thermocouple sets. The temperature difference between the reference and measuring junctions was varied stepwise from -10 °C to 10 °C (N = 19). The test results were subjected to regression analyses of the following form:

thermocouple output (μV) = slope x temperature difference (°C) + intercept (μV)

S.E. = standard error

Thermocouple set	Slope (S.E.)	Intercept (S.E.)	F-value
1	36.2 (0.1)	- 1.4 (1.2)	6.91×10^4
2	36.4 (0.1)	-10.2 (1.2)	7.76×10^4
3	36.6 (0.1)	15.9 (1.0)	1.06×10^5
4	36.1 (0.1)	5.8 (1.1)	8.53×10^4

was situated at the highest vertical limit of the crown, approximately 1.5 m above the ground. The 'windward' shoot was at the extreme windward limit of the tree, about 0.3 m above the ground. The 'sheltered' shoot was at the extreme leeward limit of the tree, about 0.5 m above ground level. The three reference junctions were housed in an tubular, reflective shield, aspirated with a small fan (Micronel Miniature Fans; type V241L). This was to avoid errors in differential temperature measurements which would arise from the reference junctions being heated by solar radiation, if they were exposed to it. The radiation shield was mounted on a photographic tripod, roughly 1 m above the upper limit of the tree's foliage.

5.2.2. Radiation measurement

Net radiation was measured with a miniature net radiometer (Swissteco Pty. Ltd.; type ME-1) held in a horizontal position about 1 m above the foliage by means of a photographic tripod. This instrument was chosen because it is relatively small, lightweight and portable. The manufacturer's supplied calibration was used.

5.2.3. Wind speed and direction measurement

Wind speed was measured using a cup anemometer (Vector Instruments, Rhyl; type A100R). This instrument was chosen partly because of its small size, yet robust construction, and partly because of its mode of operation. The spindle, on which the rotor is mounted, carries a magnet. Once every revolution the magnet operates a reed switch, causing the switch contacts to close. Thus wind speed is proportional to the rate of switch opening and closure. The advantage of this method of sensing speed of rotation is that the anemometer does not need its own power supply in order to function.

The anemometer was supplied with a manufacturer's calibration, but this was checked by comparison with a pitot static tube and micromanometer (Combustion Instruments; model 'Combist') in the Dept. of Forestry and Natural Resources wind tunnel (for a description see Thompson, 1975). A highly linear relationship was obtained between the readings of the cup anemometer and the pitot tube, but compared to the manufacturer's calibration the cup anemometer was under-reading by 2%. This was considered negligible, bearing in mind the widely-known over-running errors inherent in rotating cup

anemometers, thought to range from 1% to 10% (Kaganov and Yaglom, 1976).

As there was no wind-vane available it was necessary to improvise. The wind direction was checked every ten minutes by throwing a handful of dry grass into the air and determining its direction of travel with a compass. Although this can only be regarded as a semi-quantitative method it would have enabled detection of any major change in wind direction. This was all that was required to ensure that the 'windward' and 'sheltered' sides of a tree remained so, for the duration of a series of measurements.

5.2.4. Recording equipment - the voltage integrator

Ten minute average readings were recorded from the three thermocouple sets and the net radiometer with a home-constructed four channel voltage integrator. This unit is described in detail below. Some of the same circuitry was utilised to build a separate unit to record a ten-minute count of the anemometer contact closures (i.e. revolutions). This is also described below.

5.2.4.1. Factors affecting the choice of recording equipment

The following factors were considered when making the choice of recording equipment.

1. It had to be able to record analogue voltages and allow the determination of average readings. Spot measurements were rejected on account of the likely large variability in the instantaneous values of wind-speed, radiation and bud temperature. It is desirable to be able to measure all variables simultaneously. This cannot be achieved by one observer making spot measurements and recording them manually.

2. Because of the previously-mentioned transport constraints the equipment had to be small and lightweight.

3. The site chosen for the work was remote from mains power, so it was necessary to use battery-powered equipment. This dictated the choice of a device with a low power consumption.

4. A low budget imposed a strict limitation on the cost of the equipment.

Bearing in mind the above, it was decided to construct a four channel integrator unit, specially designed for this study. The resulting unit met the design criteria, but its construction proved to be a time-consuming enterprise.

5.2.4.2. Principle of operation

The basic idea of a voltage integrator is that it continually integrates the incoming signal and stores the current value for the integral. The integral over any given time period can be used to calculate the mean value of the incoming signal over that period. Other workers have developed voltage integrators to integrate net radiation (Saffell et al, 1979; Burgess and Cox, 1975), temperature and photosynthetically active radiation (Woodward and Yaqub, 1979). The unit described below is developed from that of Saffell et al (1979). The most important difference is that it is bipolar, i.e. able to integrate a voltage liable to intermittent changes in polarity. This feature is essential when integrating the output voltage from differential thermocouples. The input stage was completely replaced with a high gain amplifier able to cope with the small voltages produced by thermocouples. Some of the integrated circuits in the integrator stage were replaced with low power equivalents.

Figure 5.2 is a flow diagram (see appendix III for circuit diagrams) showing the basic operation of a single channel of the integrator unit. The first stage consists of a bipolar amplifier which amplifies the voltage input to provide a suitable signal for the two voltage-to-frequency converters (VFCs). On the channels used to integrate thermocouple outputs the gain was 2000, while a lower gain of 100 was used on the net radiometer's channel. Only one VFC is active at any time, depending on the polarity of the input voltage. The appropriate VFC produces a series of pulses whose frequency is directly proportional to the absolute value of the input voltage. A low-power, LCD pocket calculator is utilised as a cheap way of counting the pulses and displaying the count, which represents the integral of the incoming signal. Each pulse activates two analogue switches which simulate the contact closures caused by the depression of two calculator keys. Every pulse produced by the VFC for positive input voltages effectively 'depresses' first the

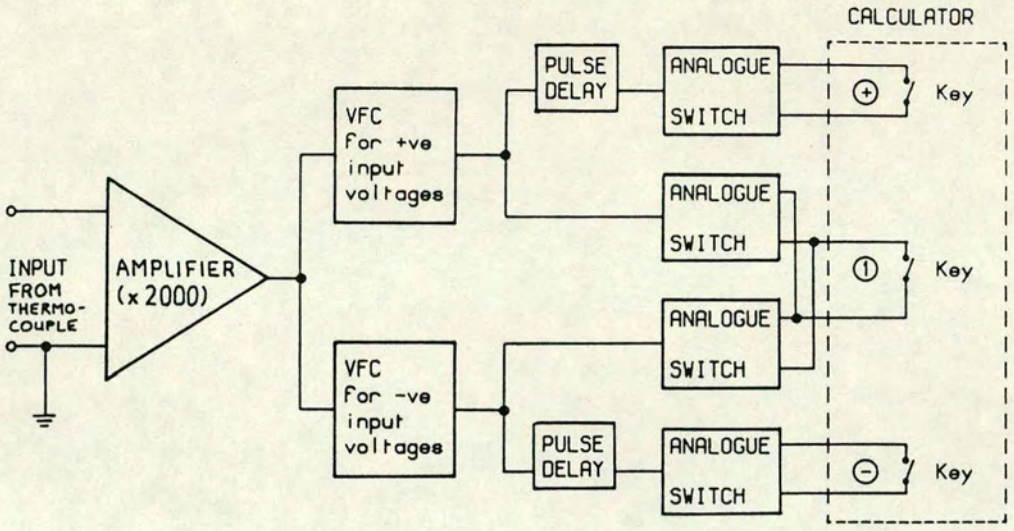


Figure 5.2. Block diagram of the integrator circuitry.

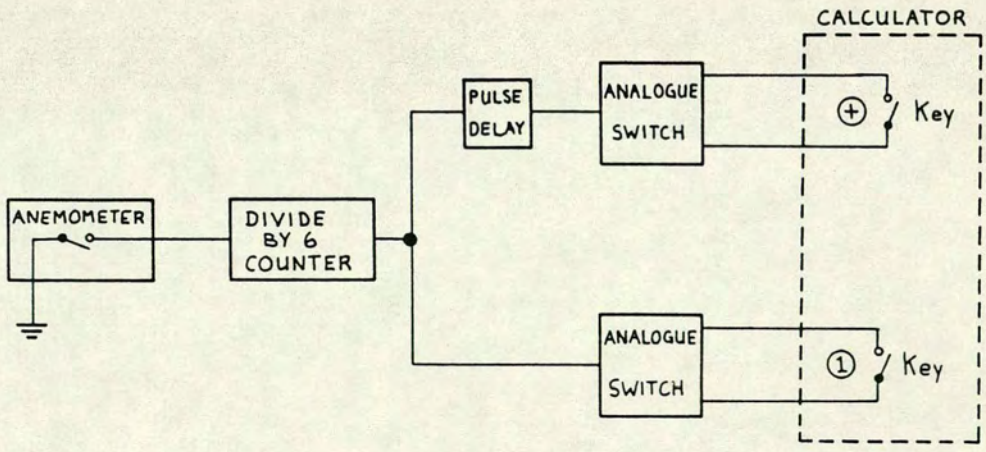


Figure 5.3. Block diagram of the anemometer counting circuitry.

'1' key, then the '+' key, thus incrementing the total count on the calculator display by one. Each pulse from the VFC for negative voltages effectively operates the '1' and '−' keys, thus decrementing the total by one. The ability of the circuit to count up or down according to the polarity of the input voltage permits integration of signals of fluctuating polarity.

5.2.4.3. Calibration and errors

To calibrate each integrator channel a voltage calibrator (Time Electronics, Kent; model 404) was employed. This unit can be programmed (by means of 'thumb wheels') to produce any desired voltage to a precision of 1 μV and accuracy of 0.05%. Input voltage was varied stepwise over the range −0.5 mV to +0.5 mV and the frequency of the pulses produced by the active VFC were measured. Frequency was determined from pulse duration, measured with an electronic timer (Racal-Dana; model 9901) having a precision of 0.001 s and accuracy of 0.03%. This method of determining counting frequency is faster and more accurate than letting the integrator run for a period of time and using the recorded count to calculate frequency (c.f. Woodward and Yaqub, 1979). The relationship between voltage input and counting frequency was found to be extremely linear.

Table 5.2b shows that the slope of the linear calibration is dependent on the power supply voltage. This highlights the fact that a stable supply voltage is essential to accurate measurement with the integrator circuit. The unit shown in plates 5.2 and 5.3 is powered by four AA-sized mercury batteries (Duracell; type ZM9) which are connected in a 'dual rail' configuration to supply +/− 2.7 volts. Mercury batteries have an extremely flat disharge characteristic, producing a stable output voltage for 90% of their life (Donnelly, 1982). They also have a high current capacity for their size, the cells used here having a capacity of 2.4 A h, allowing more than 100 hours operation of the four-channel integrator unit from one set of batteries.

The sensitivity of the integrator circuit was investigated by calibrating it at a range of temperatures in a thermostatically-controlled incubator. Table 5.2a gives the regression statistics calculated from calibration data obtained at four different temperatures from 1 °C to 30 °C. These show that temperature has a minimal effect on the calibration, and calculations (Parker, 1979) based on the 95% confidence intervals of the slopes indicate that an accuracy of ±1% of

Table 5.2

Regression statistics from integrator performance tests. During each test input voltage was varied in steps from -0.5 mV to +0.5 mV (N = 19). The test results were subjected to regression analyses of the following form:

counting frequency (Hz) = slope x input voltage (mV) + intercept (Hz)

S.E. = standard error

(a) Effect of temperature on integrator performance (power supply = +/- 2.7 V).

Ambient temperature (°C)	Slope (S.E.)	Intercept (S.E.)	F-value
1	8.29 (0.02)	-0.01 (0.00)	2.17×10^5
10	8.33 (0.02)	-0.01 (0.00)	2.36×10^5
20	8.33 (0.02)	0.00 (0.00)	1.93×10^5
30	8.37 (0.01)	0.00 (0.00)	3.45×10^5

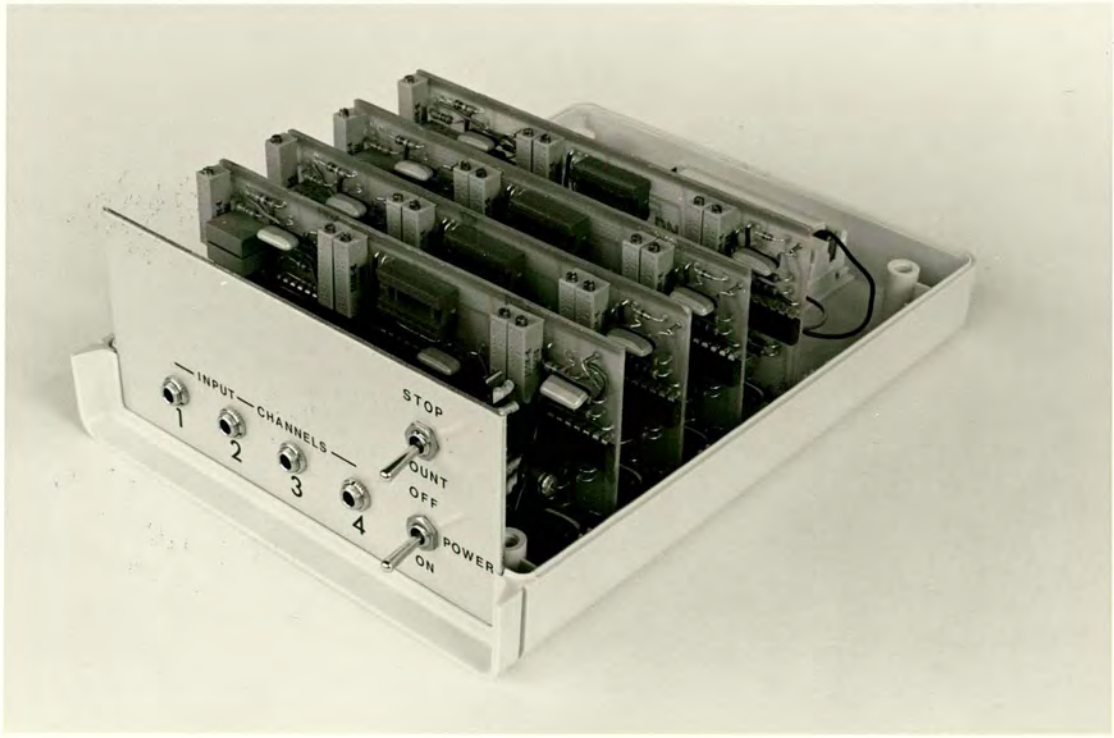
(b) Effect of power supply voltage on integrator performance (ambient temperature = 20 °C).

Power supply (+/- V)	Slope (S.E.)	Intercept (S.E.)	F-value
2.5	8.90 (0.02)	-0.01 (0.01)	1.46×10^5
2.7	8.33 (0.01)	0.00 (0.00)	3.47×10^5
2.9	7.85 (0.02)	0.02 (0.00)	2.05×10^5

Plate 5.2. Voltage integrator unit.

Plate 5.3. Voltage integrator unit, top removed.


STOP
COUNT
OFF
POWER
ON
INPUT CHANNELS
1
2
3
4


INPUT CHANNELS
1
2
3
4
STOP
OUNT
OFF
POWER
ON

reading can be safely assumed over the range investigated. This insensitivity to temperature results from the use of a monolithic chopper-stabilised operational amplifier (Intersil; type 7650) for the input stage. This amplifier possesses a minute offset voltage with a very low temperature coefficient. Metal film resistors were used throughout because of their low temperature coefficient of resistance.

A separate unit was constructed to count the anemometer contact closures. A calculator was again used to store and display the count, and the same circuitry as above was used to drive it. It was necessary to divide the contact closure frequency of the anemometer by 6, as the maximum counting rate of the calculator was found to be 4 Hz. At high windspeeds the anemometer produces contact closures at a higher rate than this maximum, thus necessitating the inclusion of the divider module. Figure 5.3 is a block diagram describing the functioning of the unit. A circuit diagram is given in appendix III.

5.3. Results

Measurements were made for different periods of time on three successive days during September 1982.

Figure 5.4 shows the data obtained on 26 September. This was an extremely windy day, with wind speed peaking at 17 m s^{-1}. The level of net radiation fluctuated widely due to intermittent heavy clouding. Despite the high windspeed a peak bud-to-air temperature differential of close to 2 °C was observed for the 'sheltered' shoot, coincident with the peak value of net radiation. The buds of the 'apical' and 'windward' shoots never achieved temperatures more than 0.3 °C above ambient air.

Figure 5.5 depicts the data recorded on 27 September. The sky was completely cloudless for the entire duration of the measurements. The wind speed was still high, with a mean magnitude of about 9 m s^{-1}. The bud-to-air temperature differentials for all three shoots were much greater than on the previous day, the differential for the 'sheltered' shoot climbing steadily to nearly 4.5 °C, achieved by 15:00 hours. At this time the difference in temperature between the windward and leeward sides of the tree was just under 3 °C.

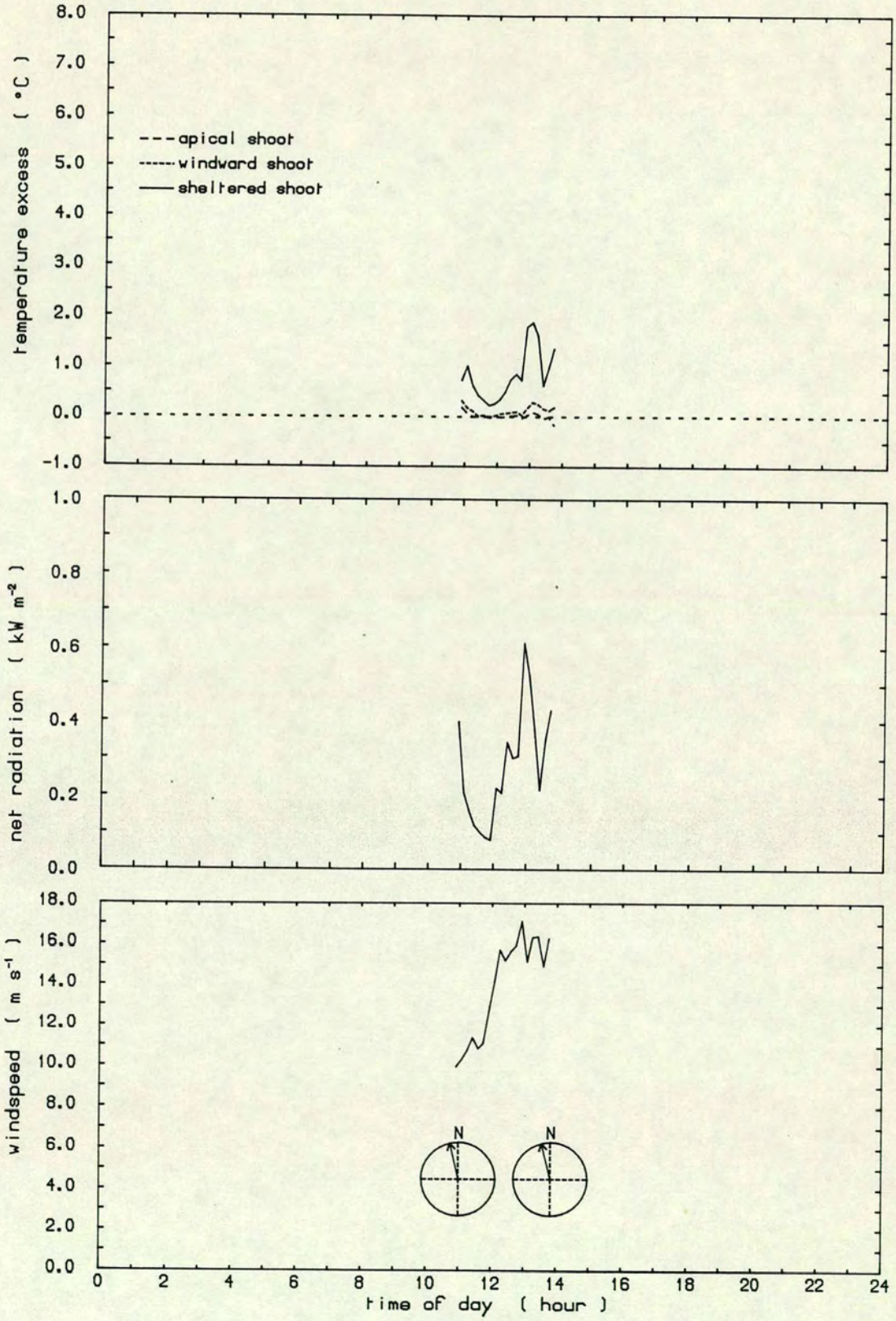


Figure 5.4. Temperature excesses recorded in *Pinus cembra* on Mt. Patscherkofel, 26 September 1982, an extremely windy day.

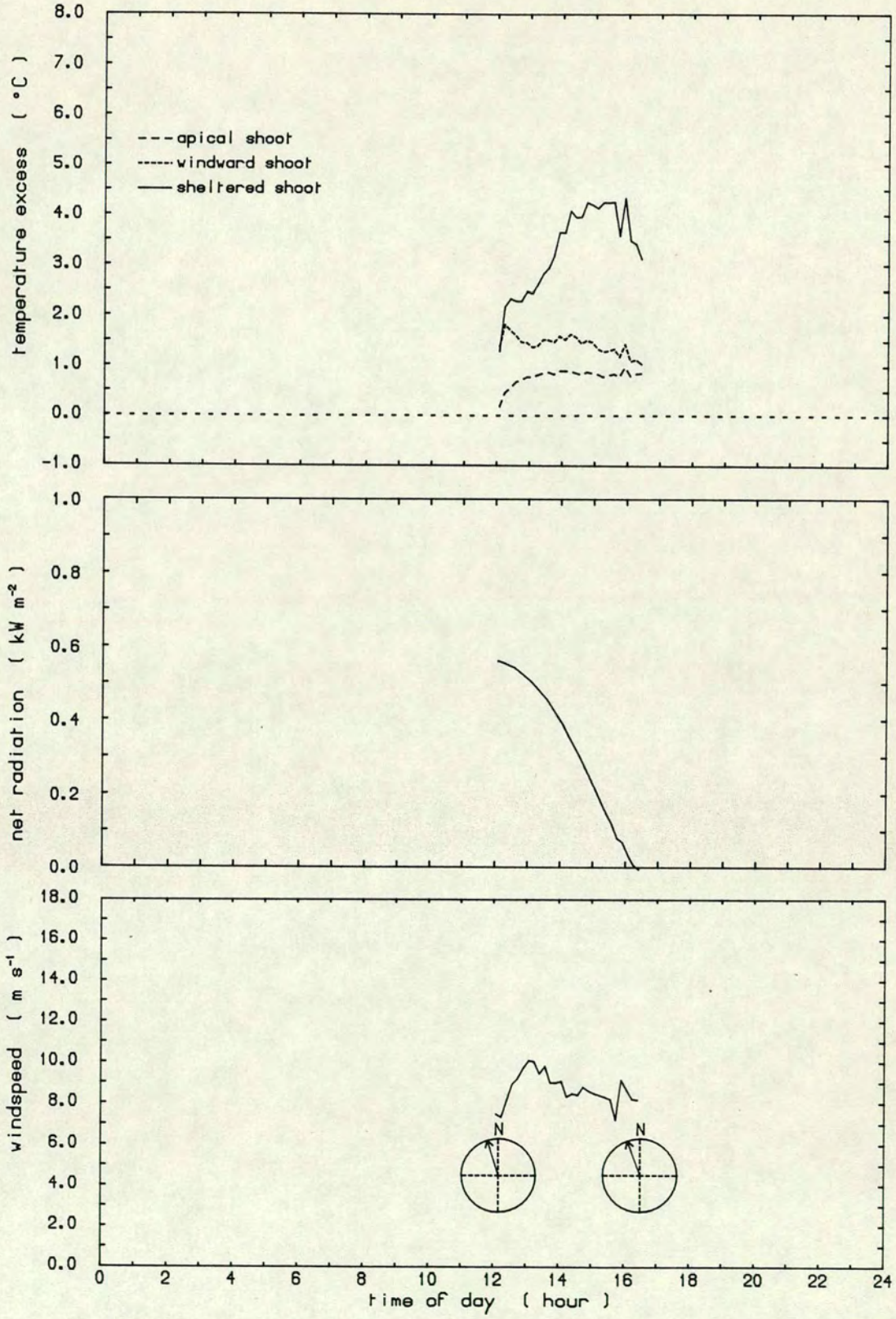


Figure 5.5. Temperature excesses recorded in *Pinus cembra* on Mt. Patscherkofel, 27 September 1982.

The data obtained on 28 September are given in figure 5.6. The windspeed was relatively low, fluctuating around 2 m s^{-1}. There was intermittent light clouding, causing some fluctuation in the level of net radiation. Under these conditions, the highest bud-to-air temperature differential of the trip was recorded - 6.7 °C for the sheltered shoot. For most of the period of measurement the buds of the sheltered shoot were about 3 °C hotter than those of the windward shoot. The apical shoot was consistently below the temperature of the others.

5.4. Discussion

The data given above show certain general trends predicted by energy balance theory (section 5.1.1). There is a clear relationship between the degree of exposure to the wind and the measured bud-to-air temperature differential. This is an inverse relationship; the greater the wind exposure the smaller the temperature differential; on the day with the highest recorded wind speed, the differentials were at their lowest for all shoots.

A qualitative relationship is also evident between net radiation and the bud-to-air temperature differentials. This is indicated by the strong tendency for temporal coincidence between peaks of net radiation and temperature differential.

However, the correlation between absolute values of net radiation and temperature differential is much less good. This is shown particularly well by the measurements made on 27 September; as net radiation declines steadily after midday, the bud-to-air temperature differentials increase or remain stable. This is not predicted by equation 5.5 above, which indicates a direct proportionality between net radiation and bud-to-air temperature differential.

The explanation for the poor agreement between theory and observation probably lies in the difference between the surface geometries of the net radiometer and the Arolla pine buds. The net radiation sensor behaves as a horizontal absorbing plane, showing a cosine response to solar elevation. Thus, on a clear, sunny day, the recorded value of net radiation declines as the afternoon proceeds. The radiation geometry of a bud is far more complex. Plate 5.4 shows a longitudinal section through a shoot of Arolla pine. The needles of this species are particularly long and densely-packed, so that the

Plate 5.4. Section of *Pinus cembra* shoot to show shelter of the apex by the needles.

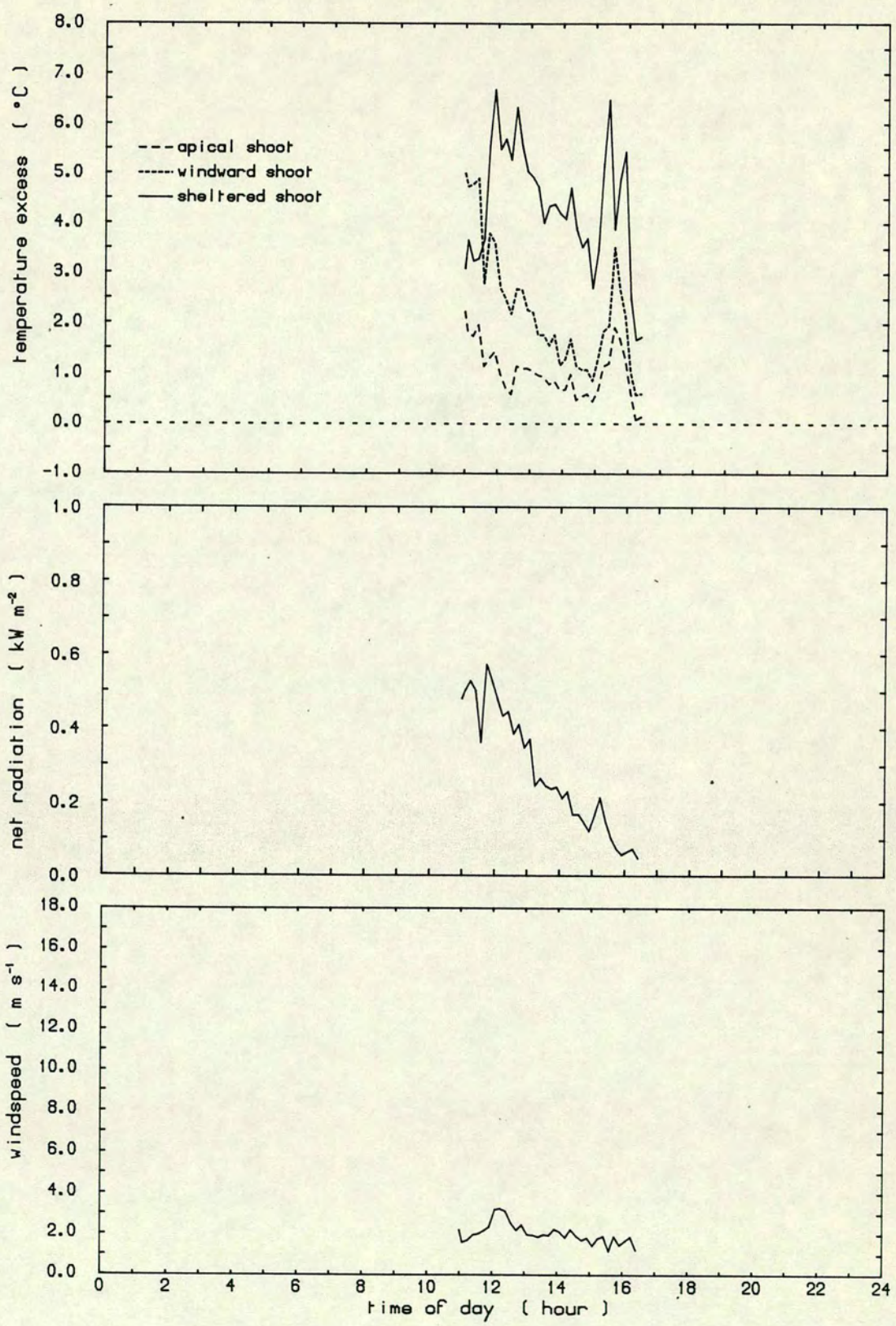


Figure 5.6. Temperature excesses recorded in *Pinus cembra* on Mt. Patscherkofel, 28 September 1982, during light wind conditions.

terminal bud is almost completely shielded by them. Little radiation exchange can occur directly between the bud and the sky or the bud and the ground. Rather, radiation exchanges occur between the needles and the environment. The bud is coupled to the needles by radiative, convective and possibly conductive exchanges of heat. The needles are orientated at many different angles around the bud, forming a complex surface, whose absorption of radiation is almost independent of the angle of incidence of the sun's rays. Thus late on a clear sunny afternoon, although the net radiometer senses little radiation, because of the sun's low angle in the sky, the shoot actually absorbs almost as much radiation as it does at noon, and therefore exhibits a high bud-to-air temperature differential.

The indirect manner in which a bud exchanges heat with the environment may cast doubt on the accuracy of theoretical calculations predicting bud-to-air temperature differentials on the assumption that the bud is a dry system. If the needles surrounding the bud are transpiring, this will use up some of the energy absorbed as net radiation, keeping their temperature closer to the air, thus reducing the amount of heat to be exchanged with the bud. In other words, although the bud may not itself transpire, its temperature may be reduced by the presence of transpiring needles around it. To some extent this is supported by the bud-to-air temperature differentials recorded for the sheltered shoot on 27 September. From noon to 15:00 hours the differential climbs from 2 °C to 4.5 °C, despite the fact that the wind speed increased slightly, and recorded net radiation decreased. This suggests that either the shoot began the day covered with a film of liquid water, which did not completely evaporate away until 15:00, or that the stomata of the needles gradually closed, reaching full closure at that time. It is hard to provide any other explanation for the steady increase in bud-to-air temperature differential in the absence of either an increase in net radiation, or a decrease in wind speed. A rapid increase might have been caused by the removal of shading by another shoot as the sun passed across the sky.

During the period of time over which measurements were made, the buds of the sheltered shoot were generally warmer than those of the more exposed shoots. The sheltered buds experienced their maximum temperature advantage (say 3 °C) on a day of low wind speed and moderate clouding. It seems likely that on a clear, sunny day, with similar low windspeeds, the temperature

difference between the sheltered and exposed buds would be even greater. The differences that these measurements have shown can occur would perhaps be large enough to be responsible for the greater growth of the sheltered side of the tree, but only if they persist for a significant proportion of the time. In a location where high wind speeds and low net radiation must often be experienced, measurements of much longer duration are necessary to ascertain whether the temperature differences are persistent or rare. If the former is found to be the case then temperature differences and their enhancement of the growth of the sheltered side of the tree could really be important in the wind-shaping process.

The magnitudes of the temperature differences are consistent with those reported by Tranquillini and Turner (1961) for Arolla pines growing at the same site. They used a resistance wire to sense the temperature of the shoot system over an entire season. Large differences between the temperature of the shoot and the air were found to occur frequently (the extreme was 21.5 °C). The observation of such large temperature excesses is not, however, in agreement with the claim of Jarvis *et al* (1976) that under normal conditions of ventilation within coniferous forest canopy,

> "needle temperatures of more than 2 °C above air temperature are most unlikely, even with closed stomata and strong radiation on the needles."

The reason for the discrepancy seems to lie partly in the differences in structure of coniferous species (different needle sizes and packing), and partly in the location of sensors.

When sensors have been attached to single needles (e.g. Yamaoka, 1958; Vanderwaal and Holbo, 1984) the observed temperature differentials are always less than 3 °C. If, on the other hand, the temperature of the bud or whole shoot is being sensed, the differentials are larger, because the effective aerodynamic dimension (d in equation 5.6) is much greater than that of a single needle.

Studies using flow visualization techniques (Wilson & Crowther, 1985) show that the shoots of coniferous foliage behave as porous bluff bodies, so that much of the air impinging on them is deflected around the entire shoot, whilst part of

the air filters through. In Arolla pine the needles are long, and there are five needles per fascicle. The fascicles appear to be much more tightly packed than in many other conifers (see plate 5.2). It may well be, therefore, that the shelter factor between windward and leeward surfaces of the shoots, and of the plants as a whole, is considerably more than in most other species.

CHAPTER 6

MEASUREMENTS OF BUD TEMPERATURES AT AN UPLAND SITE IN SCOTLAND

6.1. Introduction

The measurements in Austria showed that quite large temperature differences sometimes exist between the buds of the exposed and sheltered sides of a tree. However, measurements were only made on three days, under weather conditions liable to favour the existence of temperature gradients i.e. high irradiance. Although temperature gradients may exist briefly, it is necessary to demonstrate that they exist for a significant period of time before it can be considered likely that they actually account for asymmetrical development of the crown. The work described in this chapter was undertaken to determine the proportion of time over which temperature gradients exist. This required monitoring shoot apex temperatures over a period of time long enough to sample as broad a range of weather conditions as possible. Measurements of apical temperatures experienced by the shoots of Sitka spruce (*Picea sitchensis*) were made on 130 days at an upland site in Scotland. Some environmental variables were measured simultaneously to gain a quantitative understanding of the conditions favouring the existence of thermal gradients.

As the main aim of the work reported in this chapter was to assess the long-term temperature differences between apices of differing exposure to the wind, it would not have been sufficient to measure only the apex-to-air temperature differentials. If the absolute temperatures of the apices are known, then long-term integrals and averages of temperature can be calculated. Comparison of these quantities with published work on the temperature responses of tree growth can provide an insight to the significance of any observed variation in temperature between apices of differing exposure. Thus, in order to allow the calculation of absolute bud temperature, air temperature was measured in addition to apex-to-air differentials.

The field site and trees used for the measurements have been described previously in section 2.1.1.

6.2. Methods

The measurements reported in this chapter are similar in concept to those of chapter 5, but some changes in method were made for various reasons, detailed below. Of most significance was the use of a solid-state data-logger, which became available in 1983. This unit was able to operate unattended for periods of days or weeks, recording and storing data from a range of sensors. This gave it a great advantage over the voltage integrator unit (described in chapter 5) where the operator must be in continuous attendance if successive, short-duration integrals are required (e.g. to calculate ten-minute averages). Figure 6.1 is a block diagram showing the system of instruments used for the measurements. Plate 6.1 is a view of the site, showing the instruments and one of the trees whose apical temperatures were recorded. Below, each component of the system is described in detail.

6.2.1. Temperature measurement

Apex-to-air temperature differentials were measured with sets of thermocouples similar to those described previously in section 5.2.1. The average apex-to-air differential of a sample of four apices per branch was measured for four branches of contrasting exposure to the wind. Three series of measurements were made, a different tree being used for each. The series will subsequently be referred to as 'September-October 1983' (22 days of reliable data), 'June-July 1984' (43 days' data) and 'August-September 1984' (16 days' data). Figure 6.2 shows the location in each tree of the branches selected for study over each of the three measurement periods. For the September-October 1983 and the June-July 1984 series the four branches selected in each case occupied the same whorl. The aim was to investigate the relationship between wind-direction and the temperatures experienced by shoot apices of branches of different orientation (i.e. pointing in different directions). For the August-September period the branches selected were at different heights, thus permitting investigation of the vertical distribution of bud temperature.

The thermocouples were attached to the buds in the manner described previously (section 5.2.1) for the duration of the September-October 1983 and August-September 1984 measurements, as buds were present at the shoot apices. The June-July 1984 measurements began at a time of active shoot

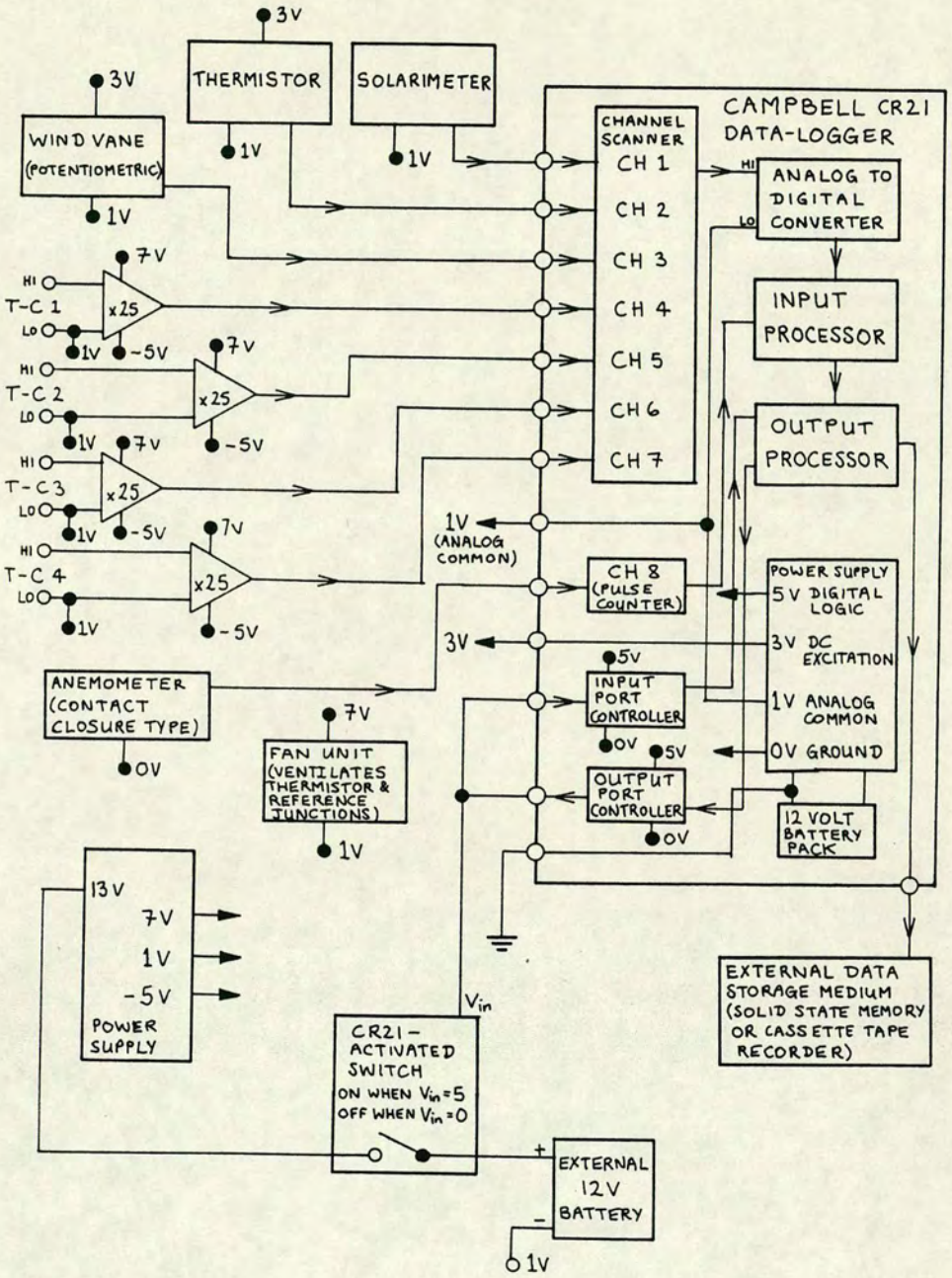


Figure 6.1. Block diagram of the data acquisition system.

Plate 6.1. View of site and instruments at Dunslair Heights. The arrowed tree is instrumented with thermocouples.

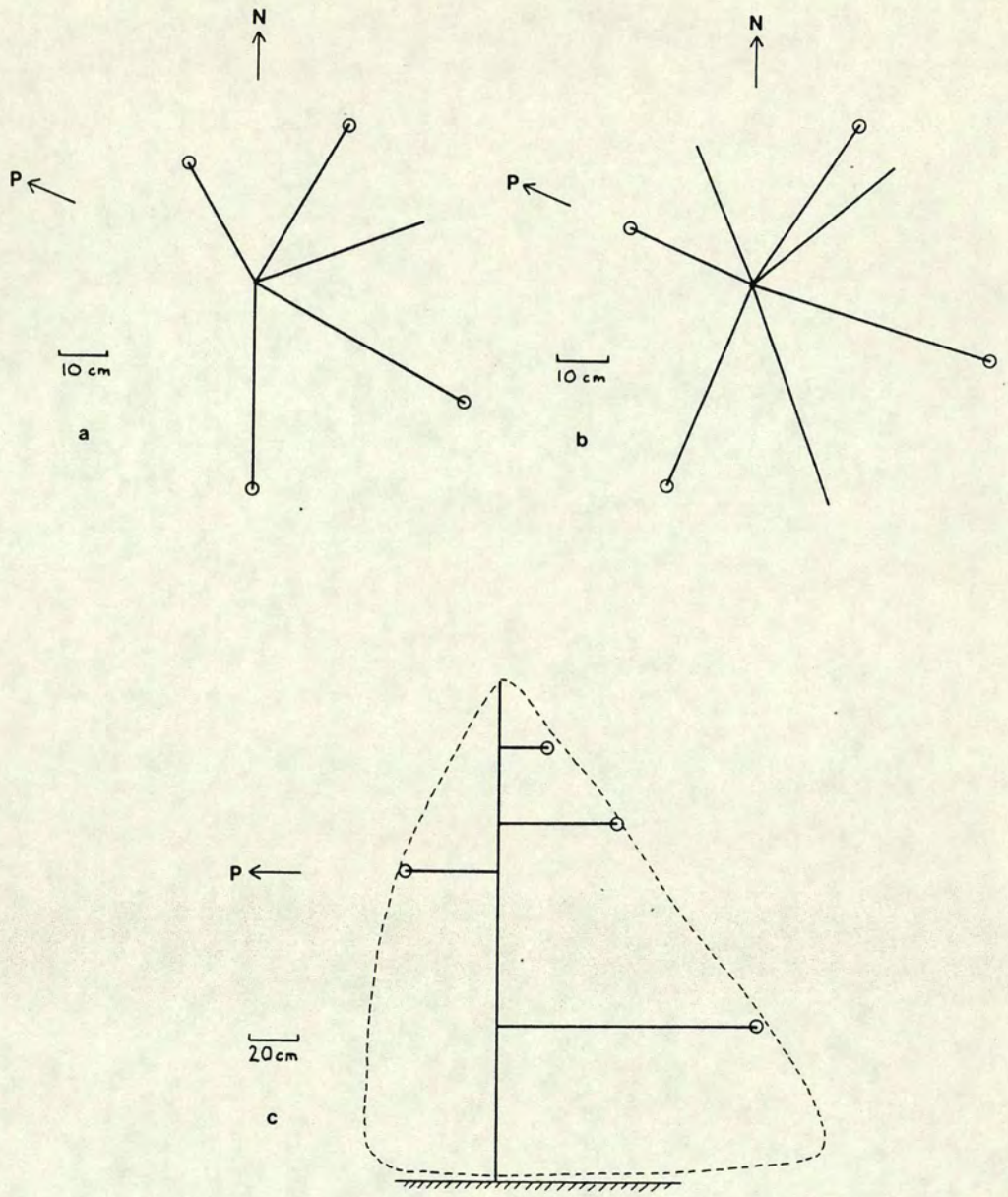


Figure 6.2. Diagrams showing the position of shoots used for measurements of shoot apex-to-air temperature differentials. Open circles indicate branches where the mean temperature differential for four shoot apices was sensed with parallel thermocouple junctions. 'N' indicates magnetic north and 'P' indicates prevailing wind direction.

(a) Plan view of 3-year-old whorl of branches used for measurements during September-October 1983.

(b) Plan view of 3-year-old whorl of branches used for measurements during June-July 1984.

(c) Side view of tree used for measurements during August-September 1984. Dotted line indicates the approximate limit of the crown.

extension, when buds were not present at the shoot tips. Each thermocouple was inserted into an axial hole in the apex, which had been carefully bored with a sewing needle. The insertion of the thermocouple did not terminate extension, which proceeded at a slightly reduced rate. By the end of the measuring period, buds were forming at the apices of the shoots containing thermocouples. The thermocouples stayed in position for most of the time, although some became detached or were broken during periods of very strong winds.

6.2.1.1. Description of measurement system

The core of the temperature measuring system was a specially-constructed unit subsequently referred to as the 'temperature unit'. This unit was designed to operate with up to four sets of parallel thermocouple junctions. Figure 6.3 shows a plan of the unit, which contained the following components:

1. Thermistor bead (RS Components Ltd., Corby; stock no. 151-243) to sense air temperature. This was housed in a ventilated tube passing through the unit. A small electric fan (Micronel Miniature Fans; type V241L) was used to produce a constant throughput of air.

2. Four thermocouple reference junctions, maintained at air temperature. These were situated in the same tube as the thermistor (above).

3. Four copper/constantan connector sockets (Omega Engineering Ltd., Connecticut, USA; type NMP-COCO-MF) mounted in the lid of the unit. Each socket was connected to one of the reference junctions and an electronic circuit (see below), which interfaced the thermocouple output to one of the data-logger's analogue input channels. Each thermocouple set consisted of four parallel junctions connected to 10 m of copper/constantan extension cable, terminated in a copper/ constantan connector plug (Omega Engineering Ltd.; type NMP-COCO-MF) which was mated with one of the sockets in the lid of the temperature unit.

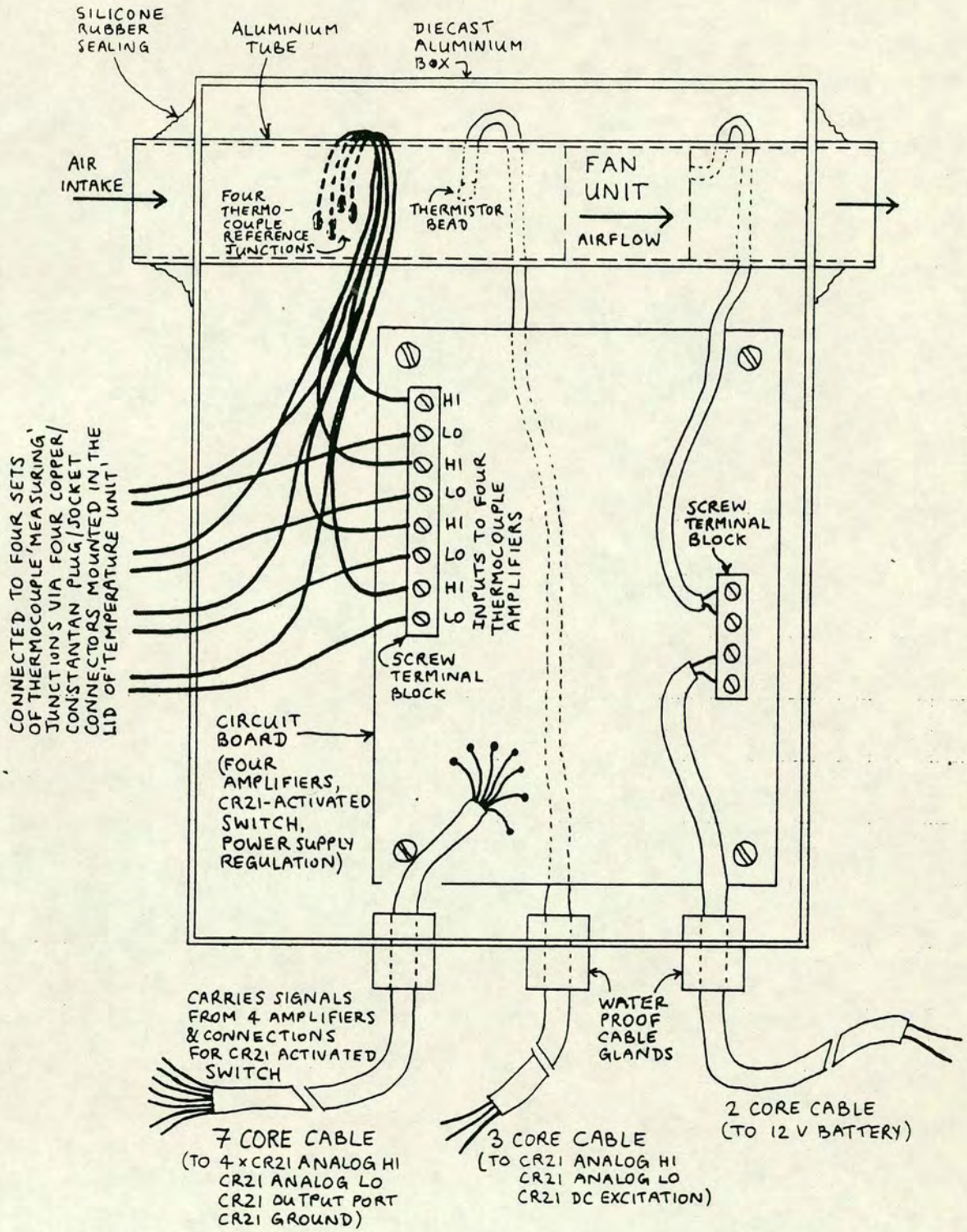


Figure 6.3. Layout of the temperature unit to show the location of thermocouple reference junctions and thermistor bead within the shielded, aspirated, aluminium tube.

This arrangement allowed a broken thermocouple set to be rapidly replaced with a spare.

4. Four thermocouple to data-logger interfacing circuits. These were amplifiers (see appendix III) which boosted the output of each thermocouple by 25 times to bring it to a level that matched the input sensitivity of the logger, thus allowing high resolution measurements.

5. Power supply unit. This regulated and modified the external 12 V battery supply to provide appropriate voltage levels for powering the four amplifier circuits and the aspirating fan.

6. Data-logger activated switch (see appendix III), allowing the data-logger to switch the whole unit on or off via a single digital signal line.

The temperature unit incorporated a variety of features designed to ensure reliable and accurate measurements. Great care was taken to prevent the ingress of moisture, which might have caused the electronic circuits to malfunction. All cables entering the unit passed through the casing via splash-proof cable glands (RS Components Ltd., Corby; stock no. 544-011). A water-proof putty (Bostik Ltd.; 'Mastik' window-sealer) was used to form a gasket around the join between the lid and the body of the unit. Other points where water could possibly enter were sealed with silicone rubber (RS Components; stock no. 555-588). The free internal space of the unit was filled with a bag of silica-gel desiccant. A removable plastic shield was fitted to the lid of the unit to protect the thermocouple connector plugs from the rain.

It was desired that the temperature of the unit should be as close as possible to ambient air temperature. Heating by solar radiation would probably have caused over-reading of air temperature and under-reading of bud-to-air differentials by warming the thermistor bead and thermocouple reference junctions, although this should have been minimised by their ventilation. A further danger was that heating by the sun might have caused temperature gradients to exist through the unit, possibly degrading the bud-to-air differential temperature measurements, by the generation of spurious

thermoelectric voltages at junctions of slightly dissimilar metals. The thermocouple connector plugs could have been particularly vulnerable to this effect, if there were differences in the exact constitution of the metals of the wires and connector pins. A secondary function of the connectors' rain shield was the prevention of temperature gradients across plugs and sockets. In an attempt to minimise heating by the sun, the entire exterior surface of the unit was covered with a reflective coating. The material chosen, an adhesive-backed, shiny, polyester film (ICI Plastics Division, Welwyn Garden City; aluminised 'Melinex') has ideal properties for this purpose. It has high short-wave reflectivity, thus reducing the absorption of solar radiation, and a high long-wave emissivity, promoting rapid heat dissipation by re-radiation.

The temperature unit was mounted on a steel mast at a height of 1.7 m, together with an anemometer and wind vane (see plate 6.2). This height was chosen to be as close as possible to the height above ground of the shoots selected for apex-to-air temperature differential measurements, thus minimising errors due to any vertical variation in air temperature.

6.2.1.2. Calibration and errors

The thermocouple sets and amplifier circuits were calibrated together in one operation. The temperature unit was placed in a thermostatically-controlled incubator (Gallenkamp, Glasgow; model INF-631W) maintained at 20 °C. The four parallel measuring junctions of each thermocouple set were immersed in a thermostatically-controlled water bath (Grant Instruments, Cambridge; model DP50). The water temperature was varied stepwise from 18 °C to 30 °C, thus producing temperature differentials between -2 °C and 10 °C. The temperature was monitored with a platinum resistance thermometer (Guildline Instruments, Canada; model 9535) with a resolution of 0.001 °C and a long term accuracy of 0.03 °C. This instrument was also used to check the incubator temperature from time to time. The outputs of the four amplifier circuits were fed directly to four analogue input channels of the data-logger, which was used to read millivolts. The resulting calibration data for each thermocouple set were subjected to regression analysis. The regression statistics are given in table 6.1. Calculations (Parker, 1979) based on the 95% confidence intervals for the slope and intercept show that for the 'worst case' (3) an accuracy of ±0.2 °C can be specified for a reading of a

Plate 6.2. The temperature unit, windvane and anemometer.

Table 6.1

Regression statistics from the combined calibration of four thermocouple sets and four amplifier circuits used at Dunslair Heights during September and October 1983. The temperature difference between the reference and measuring junctions was varied stepwise (N = 5) from -2 °C to 10 °C. The resulting data were subjected to regression analyses of the following form:

amplifier output (mV) = slope x temperature difference (°C) + intercept (mV)

S.E. = standard error

Thermocouple-amplifier combination	Slope (S.E.)	Intercept (S.E.)	F-value
1	0.974 (0.008)	0.357 (0.058)	1.51×10^4
2	0.965 (0.009)	0.397 (0.064)	1.20×10^4
3	0.980 (0.009)	0.174 (0.065)	1.20×10^4
4	1.009 (0.008)	0.046 (0.055)	1.81×10^4

Table 6.2

Regression statistics from the calibration of the thermistor used with the CR21 data-logger to measure air temperature. The temperature of the thermistor was varied stepwise (N = 5) between 5 °C and 25 °C. The resulting data were subjected to regression analysis of the following form:

CR21 reading (°C) = slope x true temperature (°C) + intercept (°C)

S.E. = standard error

Slope (S.E.)	Intercept (S.E.)	F-value
1.000 (0.003)	-0.223 (0.042)	1.40×10^5

10 °C temperature differential.

The thermistor was calibrated separately, prior to its installation in the temperature unit. It was immersed in the same waterbath as above, taking care to ensure that its leads were well insulated from one another and the water. The temperature of the water was varied in steps from 5 °C to 25 °C, and was monitored with the same thermometer as above. The thermistor was energised and read by the data-logger, which contains a linearisation program, based on a fitted polynomial curve, matching the characteristics of the type of thermistor used. The data-logger manufacturer quotes a resolution (over the range from 0 °C to 30 °C) of 0.05 °C and accuracy of ±0.09 °C for temperature measurement with the thermistor. The results of the calibration were subjected to regression analyses. The regression statistics are given in table 6.2. Calculations (Parker, 1979) based on the 95% confidence limits of the slope and intercept indicate an accuracy of ±0.1 °C.

6.2.2. Wind speed and direction measurement

Wind speed was measured with the same anemometer as previously described in section 5.2.3. The anemometer was connected to the 'fast' digital input channel of the data-logger, enabling the logger to count the contact closures and determine the wind speed.

Wind direction was measured with a potentiometric-type wind vane (Vector Instruments, Rhyl; type W200P). This instrument was chosen because it produces an output voltage which is directly proportional to the deviation (clockwise) of wind direction from the north (i.e. from 0° to 360°). A linear response to the angle of the vane is desirable as it allows the use of the logger's input processing capability to convert output voltage directly to wind direction (in degrees). It has a minimal power requirement, allowing it to be energised directly from the data-logger.

The anemometer and wind vane were mounted on a mast at a height of 1.8 m. A magnetic compass was used to align the 'north' mark on the wind vane body with magnetic north. Although this was done as carefully as possible, an error of a few degrees either way could have been made, thus introducing a maximum of (say) ±5° uncertainty into the wind direction measurement.

6.2.3. Radiation measurement

It was decided to measure solar radiation rather than net radiation. Two considerations dictated this decision.

Firstly, the solarimeter which was available, a Moll-Gorczynski-type pyranometer (Kipp and Zonen Ltd., Delft, The Netherlands; type CM3) has a more ideal radiation geometry than the net radiometer used previously in Austria. The sensitive thermopile is protected from convective cooling by a hemi-spherical glass shield, so the response of the instrument is independent of solar angle in the horizontal plane. The net radiometer's sensing element is protected by a polythene tube with opaque ends, so its measurement of net radiation is influenced by its orientation in the horizontal plane, relative to the sun. Thus accurate interpretation of its readings is rather difficult. The solarimeter, however, does not suffer from this problem.

Secondly, it may in future be possible to use the measurements of apex temperature and microclimate to construct a simple mathematical model. This model would predict the likely thermal gradient across the tree under any combination of environmental conditions. Meteorological data (from similar sites), spanning a period of several years, could be fed into the model to determine whether temperature gradients exist for a great enough proportion of the time to produce asymmetrical crown development. At Meteorological Office weather stations irradiance is usually measured with a solarimeter. It is desirable that the model should be constructed on the basis of data gathered with the same type of instrument, as this is likely to ensure the greatest accuracy for the predictions based on weather station data.

The solarimeter was exposed at a height of 0.6 m and aligned in the horizontal plane by means of a spirit level. Care was taken to select a location where the instrument would not be overshadowed at any time of day. Before each series of field measurements the solarimeter was charged with fresh desiccant (silica-gel), to prevent the formation of condensation on the inner surfaces of the glass domes.

The calibration certified by the manufacturers was used. The accuracy quoted is ±1.5% of reading.

6.2.4. Recording equipment - the Campbell CR21 data-logger

The sensors listed above were all connected to a solid-state data-logger (Campbell Scientific, Utah, USA; model CR21). This was able to operate unattended for days or weeks, taking readings from the sensors at regular intervals and storing them for later retrieval.

The CR21 has a number of features which made it an ideal choice for the work.

1. Battery powered, with an extremely low power requirement allowing approximately 5000 hours operation on one set of batteries.

2. Small, lightweight and easily portable.

3. Supplied in a rugged, weather-proof housing.

4. Able to scan 7 analogue and 2 digital input channels (all channels are read every 10 seconds).

5. Intelligent i.e. able to perform simple processing of raw data at user-programmable time intervals. The type of processing task to be performed on the readings from each channel is selected by the user. This processing capability minimises the amount of data that must be stored for later retrieval. Thus the unit can be left unattended for longer, as it takes more time for the finite capacity of the storage medium to be filled.

6. Able to energise sensors requiring power e.g. wind vane and thermistor.

7. High precision and accuracy as specified by the manufacture. The quoted accuracy (operating over the temperature range of 0 °C to 40 °C) is ±0.2% of reading or two times the resolution, whichever is the greater. On the most sensitive range for analogue voltage inputs (which was used for all sensors except the wind vane) the

resolution is given as ±5 μV.

Although the CR21 was supplied with a weather-proof housing, some extra precautions were taken to guard against the ill effects of water. All the cables going into the CR21 enclosure entered the casing through splash-proof cable glands (R.S. Components Ltd., Corby; stock no. 544-011). Bags of silica-gel desiccant were kept inside the housing, to prevent the occurrence of high humidities. Under these conditions condensation might form on the circuit boards of the logger, causing it to malfunction. The desiccant bags were replaced with fresh ones every time the field site was visited.

The sensor cables were all shielded against electrical pick-up. To ensure signal integrity and protect against lightning strikes, the cable shields and the CR21's ground terminal were connected to earth via a heavy-duty copper cable and a 1 m copper stake, sunk into the ground.

The CR21 was programmed with the calibration for each sensor, so that raw readings of voltage or digital counts could be instantaneously converted into the S.I. units of the quantity being measured. The input channels were scanned every ten seconds. The logger was programmed to compute, every ten minutes, an average value of the readings from each channel. Only these ten-minute average values were written into final memory for subsequent retrieval.

6.2.5. Data storage and analysis

The internal memory of the CR21 is quite small, only being able to store 608 final data values. At the end of each ten-minute period, the averaging process generates an array of 12 values to be held in storage. Thus the internal memory is exhausted in only 8.4 hours. In order to allow longer periods of time to pass between visits to the logger for data retrieval, it was necessary to connect some kind of external storage medium. During 1983 the only device available was a Mass Storage Unit (or 'MSU', manufactured by Systematic Micro Ltd., Ascot; model 3010) able to store a maximum of 4000 data points in random access memory.

For reasons of economy, it was considered desirable to maximise the time interval between visits to the field site for retrieval of data. Two factors

determine the length of time interval necessary. These are the time taken to exhaust the available data storage space, at the desired rate of data acquisition, and the life of the power supply. If ten-minute averages are desired, 1728 data points must be written to memory every day. Thus a memory of 4000 locations would be full after 2.3 days. The data-logger's internal battery supply lasts for 5000 hours (approximately 200 days), and the 9 A h lead-acid battery (Berec (Varley Batteries) Ltd., London; type VPT 12.7/10) used to power the temperature unit allows it to operate for 5.1 days. Memory space was thus the factor limiting the maximum duration of unattended operation.

In order to extend the period of time before memory saturation occurred, it was decided that measurements need only be taken during daylight hours. As temperature gradients of any significance (i.e. $> 1^{\circ}C$) can only exist when the magnitude of net radiation is quite large (see equation 5.12), this strategy roughly doubles the time before the storage unit is full, but does not cause the loss of any useful information. Although net radiation has a negative value at night, its absolute magnitude would never be great enough to produce a significant temperature gradient between the apices of the sheltered and exposed sides of the tree.

To gain the desirable increase in the time span of unattended operation, some means of switching the temperature unit on at sunrise and off at sunset was required. This was achieved by programming the CR21 to write data to the MSU, and power-up the temperature unit, only when the solarimeter was reading more than 5 W m^{-2} solar radiation. The power supply was switched on and off with a reed relay, controlled by one of the CR21's digital output ports. Because the digital ground line is 1 volt below the analogue input channels' common 'low', to which the temperature unit's power supply was referenced, it was necessary to design and construct a circuit which permitted switching, but maintained complete electrical isolation between the output port and the power supply. This was achieved by employing an opto-isolator (see appendix III for a circuit diagram). Using this set-up the whole system could be left unattended for up to 5 days.

To retrieve the stored data the MSU was disconnected from the CR21 and brought back to Edinburgh. Here the data could be transferred to the

University's mainframe computer by connecting the unit to a terminal, via a standard RS232 interface. A FORTRAN77 program, 'MSU2' (see appendix II) was written to control transfer of the data. Once stored in a file on the mainframe the data was amenable to numerical analysis.

Use of the MSU is inconvenient on two accounts. Firstly, in order to retrieve the stored data the unit must be transported from the field site to the nearest computer installation. Once emptied, it must be returned before further data can be stored. Hence two return journeys are necessary and, moreover, it is impossible to collect a continuous record of measurements over a long period. Secondly, the amount of storage available is rather small, so frequent visits to the field site are required, if reasonably intensive measurements are desired.

In 1984, these problems were solved by the acquisition of a tape recorder (Systematic Micro Ltd., Ascot; model RQ-356) able to store data on cassette tape and a tape reader (Campbell Scientific, Utah, USA; model C20). The tape reader decodes the data recorded on the tape, and transfers it to the mainframe computer via a standard RS232 interface. A FORTRAN77 program, 'C20' (see appendix II), was written to control the operation of the tape reader, from a computer terminal. One side of a C90 cassette can store more than 2×10^5 data values, so the exhaustion of the temperature unit's power supply became the factor limiting the time for which the system could operate unattended. In order to extend this time period, the 12 V battery powering the temperature unit was replaced by a 24 A h sealed lead-acid battery (Yuasa Battery Co. Ltd, Tokyo, Japan; type NP24-12B), capable of providing power for 13.7 days. Thus the system was able to provide an unbroken series of measurements (except in the case of component failures), as long as the site was visited at least every 13 days to replace the battery with a freshly charged one, change the cassette tape, check on the general functioning of the system and carry out necessary maintenance.

Various analyses were performed on the raw data once it was stored in computer files on the mainframe. The results of these analyses are reported in section 6.3 below. All of the graphs were prepared using a locally-available package, 'EASYGRAPH' (see appendix II). The linear regressions were calculated with a locally-available statistics package, 'PRESTO' (see appendix II). The

remaining numerical analyses were performed using FORTRAN77 programs written by the author.

6.3. Results

The first part of this section is the presentation and description of graphs showing the diurnal trends in the measured quantities for a small number of the days on which reliable measurements were obtained. These days were selected to show the behaviour of the apex-to-air differentials of the different shoots under a variety of climatic conditions.

The next part is an analysis of long-term differences in the temperatures experienced by the apices of the different shoots. Mean temperatures and frequency distributions of temperature have been calculated.

In the last part the data are analysed in the light of energy balance theory (section 5.1.1), allowing consideration of the underlying processes responsible for temperature differences between apices of differing exposure to the wind.

6.3.1. Diurnal temperature trends

Three graphs of the data obtained have been plotted for each day selected for presentation. To provide an easy visual summary of each day's data the three graphs relating to it are given on the same page. The top graph shows the diurnal variation in the average apex-to-air temperature differential of a sample of four shoots on each of a number of branches of contrasting exposure to the wind (see figure 6.2 for diagrams showing the positions of the branches where shoot apical temperatures were measured). The middle graph shows the diurnal variation in solar radiation. The bottom graph is a plot of the wind speed during the day. Wind direction is also indicated at three times of day by a 'dial'. North is marked by 'N', so the position of the arrow indicates the compass direction from which the wind was blowing, at a time indicated by the horizontal position of the dial centre, with respect to the time axis.

Figure 6.4 shows the measurements obtained on 17 July 1984. The level of solar radiation was very low throughout the day, probably as a result of the cloud base being below the elevation of the field site. Wind speed was rather high, peaking at just over 6 m s^{-1}. Under these conditions the apex temperatures were never more than 0.5 °C above air temperature and mostly

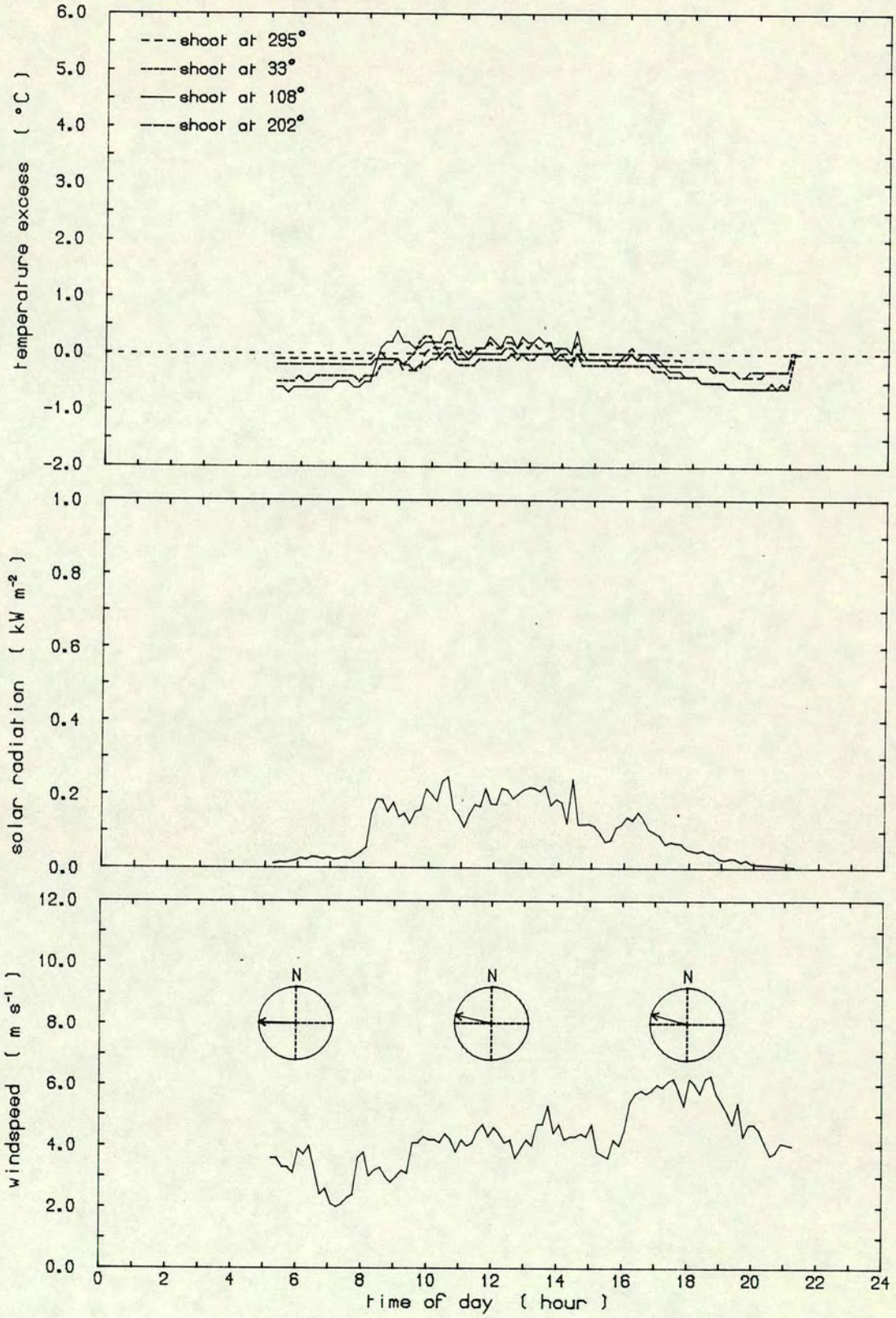


Figure 6.4. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 17 July 1984. Most exposed shoot, 295°, most sheltered, 108°.

around 0.5 °C below air temperature. There was no discernable difference between the average temperature differentials to air of the apices at different locations in the whorl.

On 25 June 1984 (figure 6.5), the apex-to-air differentials were similarly low, although the shoot most sheltered from the wind (shoot at 108°) achieved a peak differential of 1 °C. This shoot was warmer than the others for most of the day, but only by a few tenths of a degree. As the levels of solar radiation were quite high, peaking at 850 W m^{-2}, somewhat larger temperature differentials might have been expected. Their absence was probably caused by the extremely high wind speed, declining from 12 m s^{-1} to 6 m s^{-1} as the day proceeded.

Slightly lower values of net radiation (peaking at 800 W m^{-2}) and wind speed (fluctuating around 5 m s^{-1}) were observed on 13 July 1984 (figure 6.6). Under these conditions the apex-to-air temperature differentials were a little greater. The most sheltered shoot (shoot at 108°) reached a peak temperature differential of 2.2 °C and between 11:00 and 13:00 was on average about 1 °C warmer than the other, more exposed shoots. The strong temporal coincidence between peaks in solar radiation and peaks in the temperature of the most sheltered shoot should be noted.

Obvious coincidence between high levels of solar radiation and large apex-to-air temperature differentials were also observed during the afternoon of 5 July 1984 (figure 6.7). This was clearly a sunny day, but in the afternoon intermittent clouding caused wild fluctuations in the measurements of solar radiation. The wind speed was rather lower than on the days considered previously, and apex-to-air temperature differentials were high. The apices of the most sheltered shoot (shoot at 108°) were the hottest for most of the day. For the three hours preceding noon their mean temperature advantage over the most exposed shoot (shoot at 295°) was approximately 4 °C.

Large apex-to-air temperature differentials were also observed on 4 July 1984 (figure 6.8). This was a very sunny day with only a few light clouds present during the afternoon. Wind speed was very low at 5:00 hours, when the day's measurements began, but it climbed steadily, achieving a peak of 5 m s^{-1} by 16:00 hours. It is worth noting the rapid decline in apex-to-air temperature differentials that accompanied this increase in wind speed

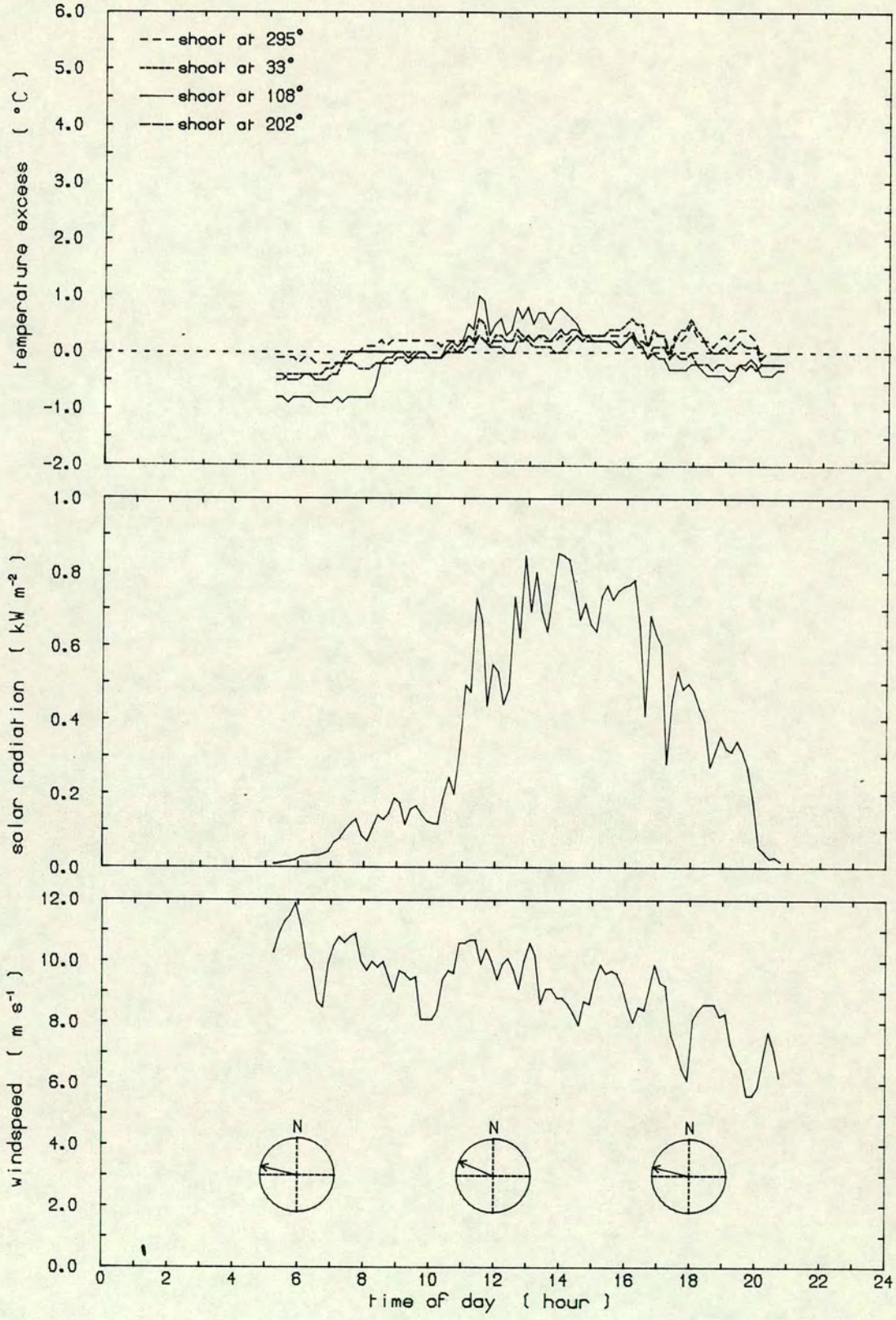


Figure 6.5. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 25 June 1984. Most exposed shoot, 295°, most sheltered, 108°.

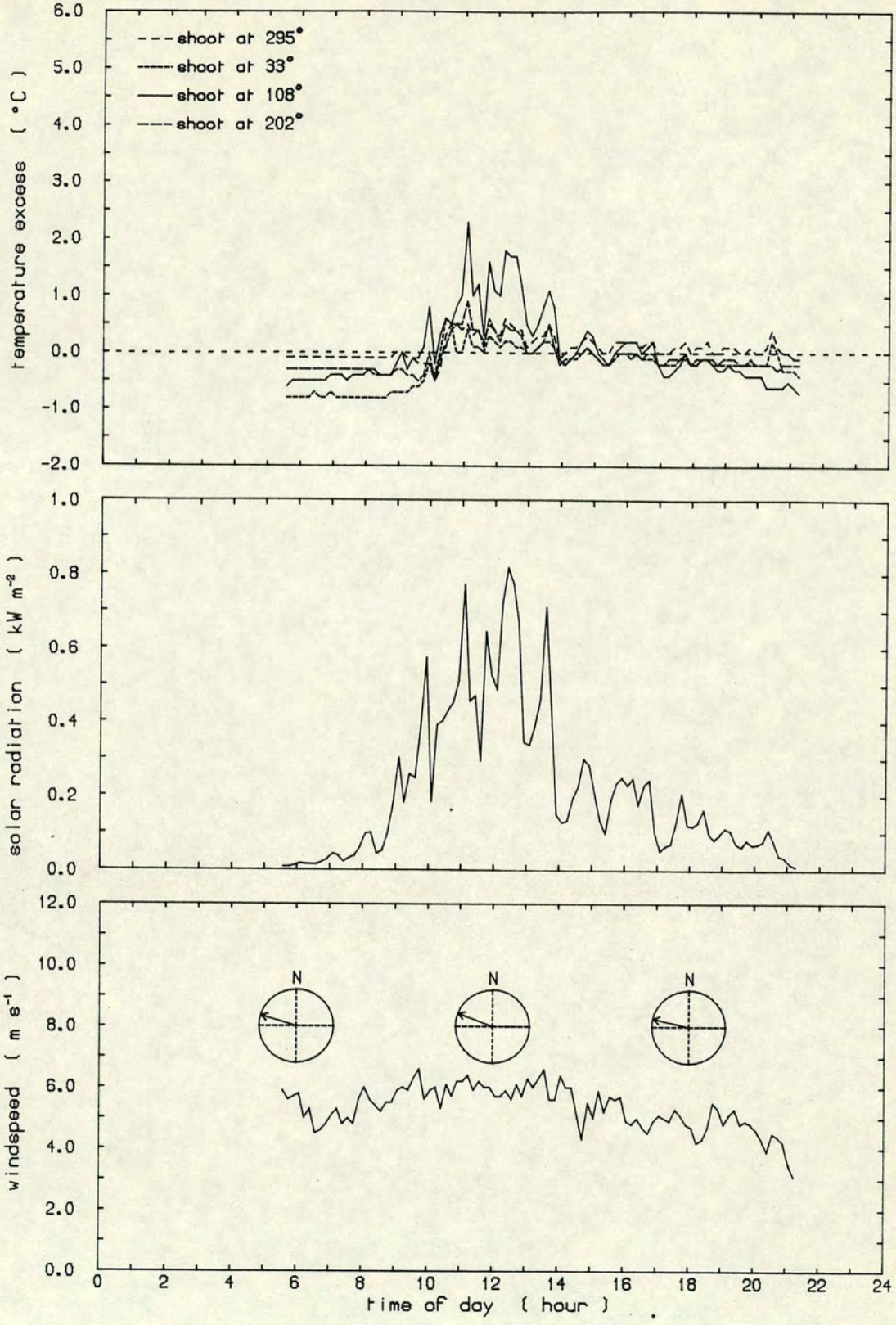


Figure 6.6. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 13 July 1984. Most exposed shoot, 295°, most sheltered, 108°.

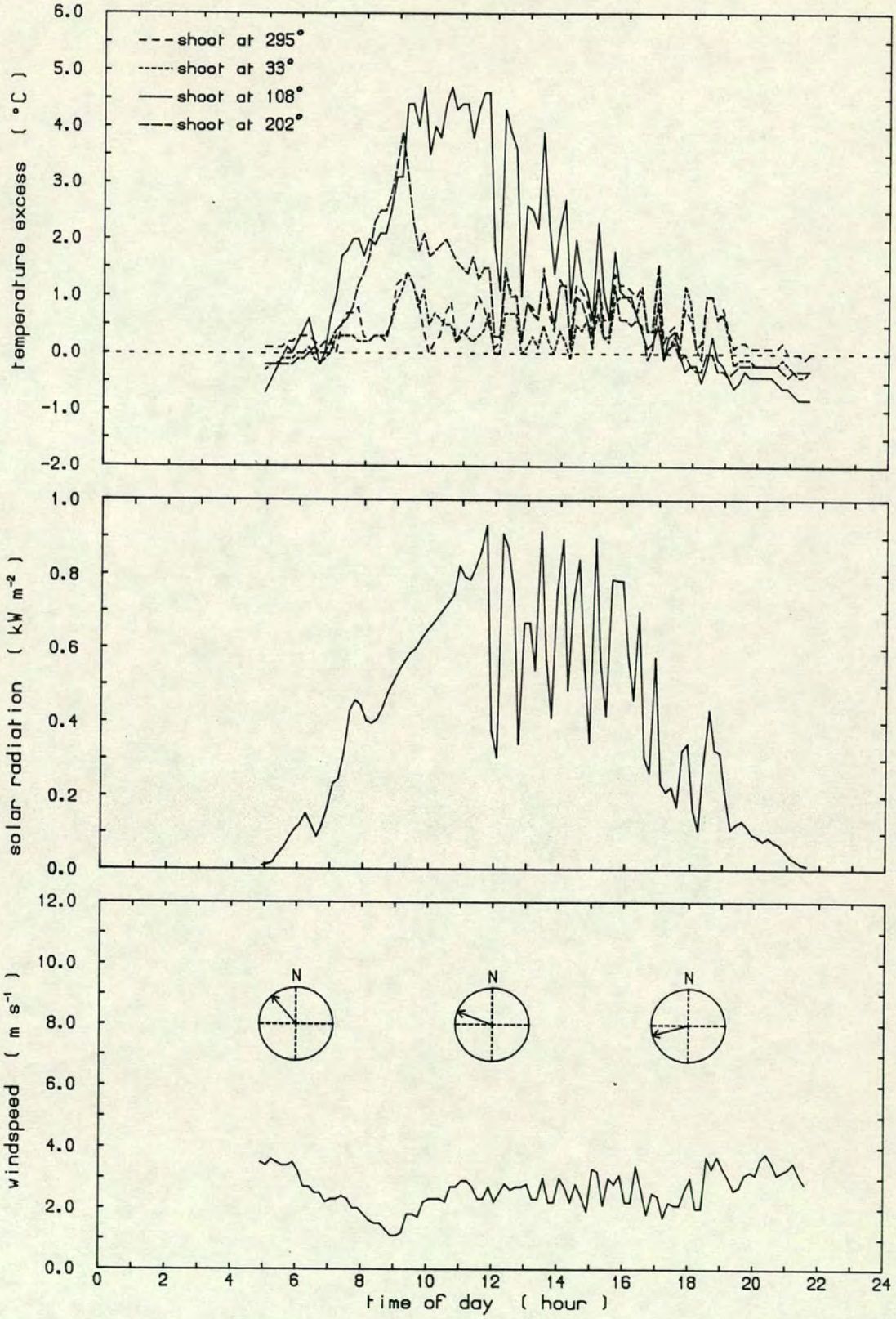


Figure 6.7. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 5 July 1984. Most exposed shoot, 295°, most sheltered, 108°.

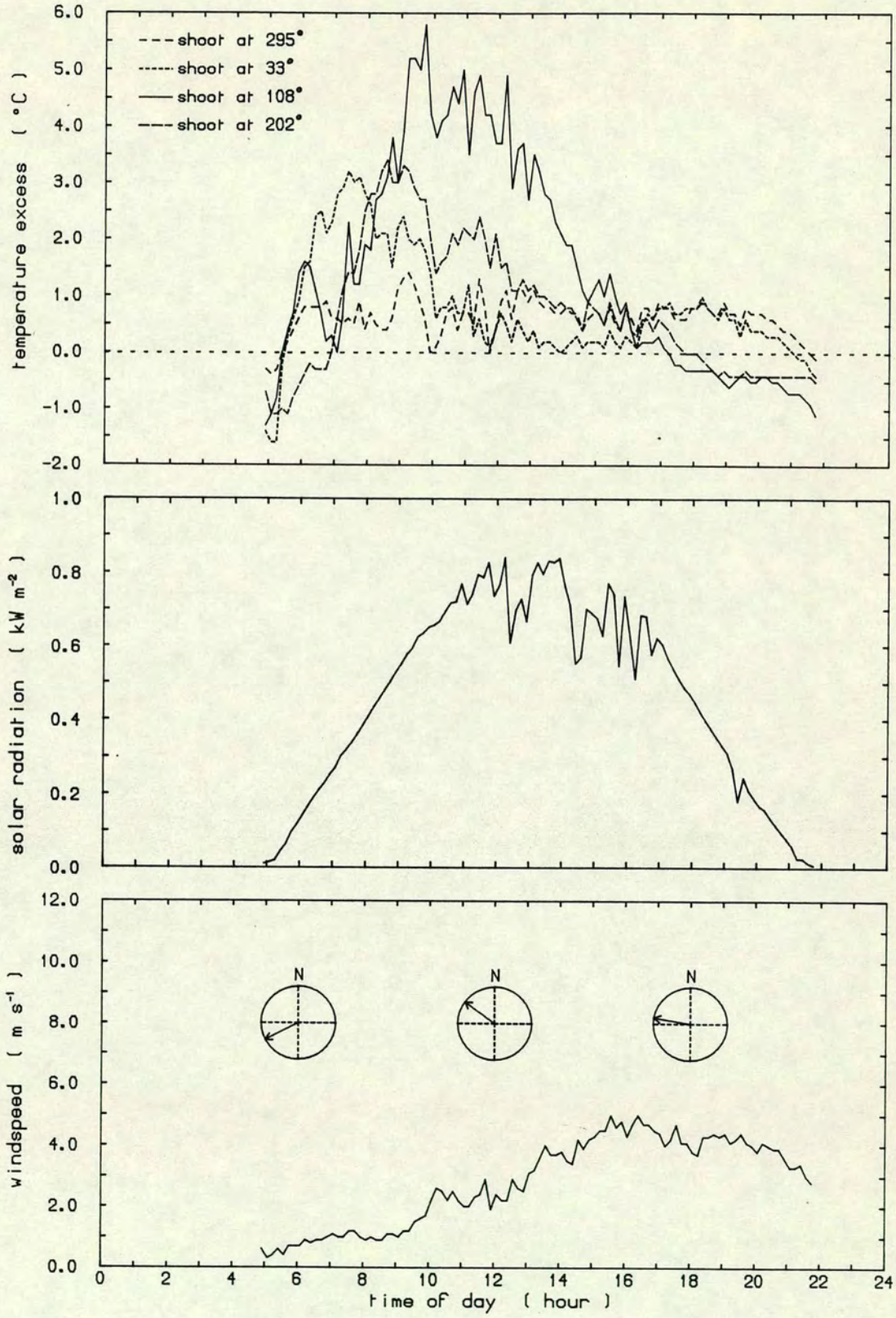


Figure 6.8. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 4 July 1984. Most exposed shoot, 295°, most sheltered, 108°.

(between 13:00 hours and 16:00 hours). Solar radiation did not decline markedly during this period. In the early morning, the shoot at 33° was the most sheltered and also the warmest, attaining a maximum bud-to-air temperature differential of 3 °C. By late morning, wind direction had changed, so that the shoot at 108° became the most sheltered for the remainder of the day. From 9:00 hours until late afternoon, this shoot was much hotter than the other shoots, experiencing a peak bud-to-air differential of almost 6 °C. Over this period there is a clear relationship between the ranking of apex-to-air temperature differentials and the degree of exposure experienced by the shoots.

The effect of rapidly veering wind direction are shown particularly clearly by the data obtained on 24 July 1984 (figure 6.9). The recorded values of solar radiation were high, the wind speed was moderate (averaging around 2 m s^{-1}), and some high apex-to-air temperarure differentials occurred during the day. At 6:00 hours the wind was blowing from 139°, so the shoot at 295° was the most sheltered. It was nearly 1 °C above air temperature at this time, just a little warmer than the other shoots. Between 10:00 and 11:00 hours the wind direction changed rapidly to 250° and continued to veer towards the north. At this time the shoot at 108° was the most sheltered and the hottest, its apices achieving a peak temperature excess above air of 5.8 °C. Until just after noon, this shoot experienced a 3 to 5°C advantage over the most exposed shoot. By 15:00 hours the wind had reached north, so the shoot at 202° became the most sheltered shoot. From 14:00 hours to 18:00 hours it was between 2 °C and 4 °C hotter than the most exposed shoot. For the remainder of the day's measurements, the wind direction fluctuated around 110°. Over this time interval the shoot at 295° was the most sheltered and warmest shoot.

Two further days' data are presented in this section. These days were selected from the August-September 1984 series of measurements, when the thermocouples were attached to the buds of shoots at different heights in the tree (see figure 6.2 for further details). This allowed investigation of the vertical distribution of temperature.

Figure 6.10 shows the data obtained for 3 September 1984. The wind speed was high, averaging 4.8 m s^{-1}, and the values recorded for solar radiation were low to moderate. Despite these conditions, some large bud-to-air

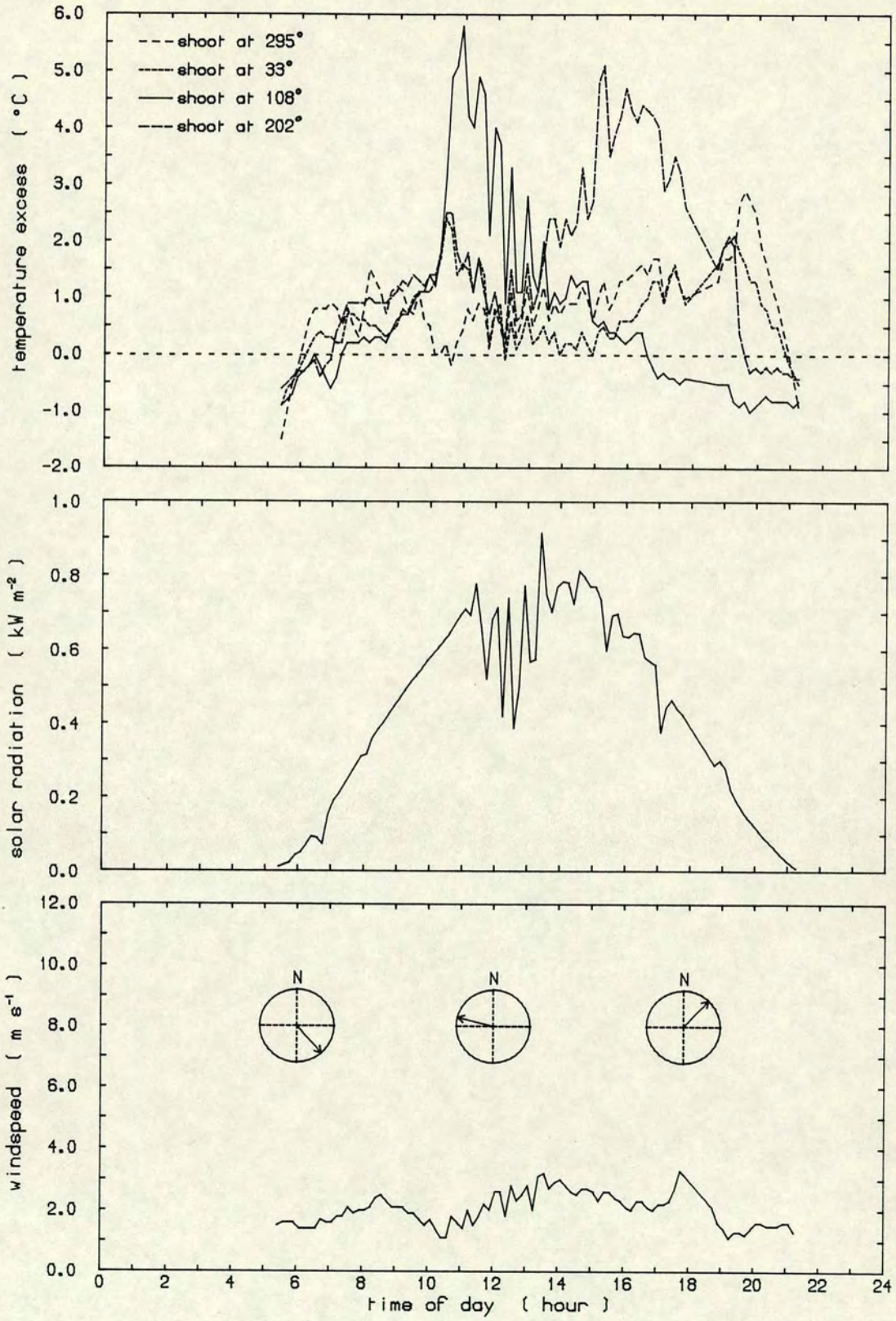


Figure 6.9. Temperature excesses on *Picea sitchensis* at Dunslair Heights, 24 July 1984. Most exposed shoot, 295°, most sheltered, 108°.

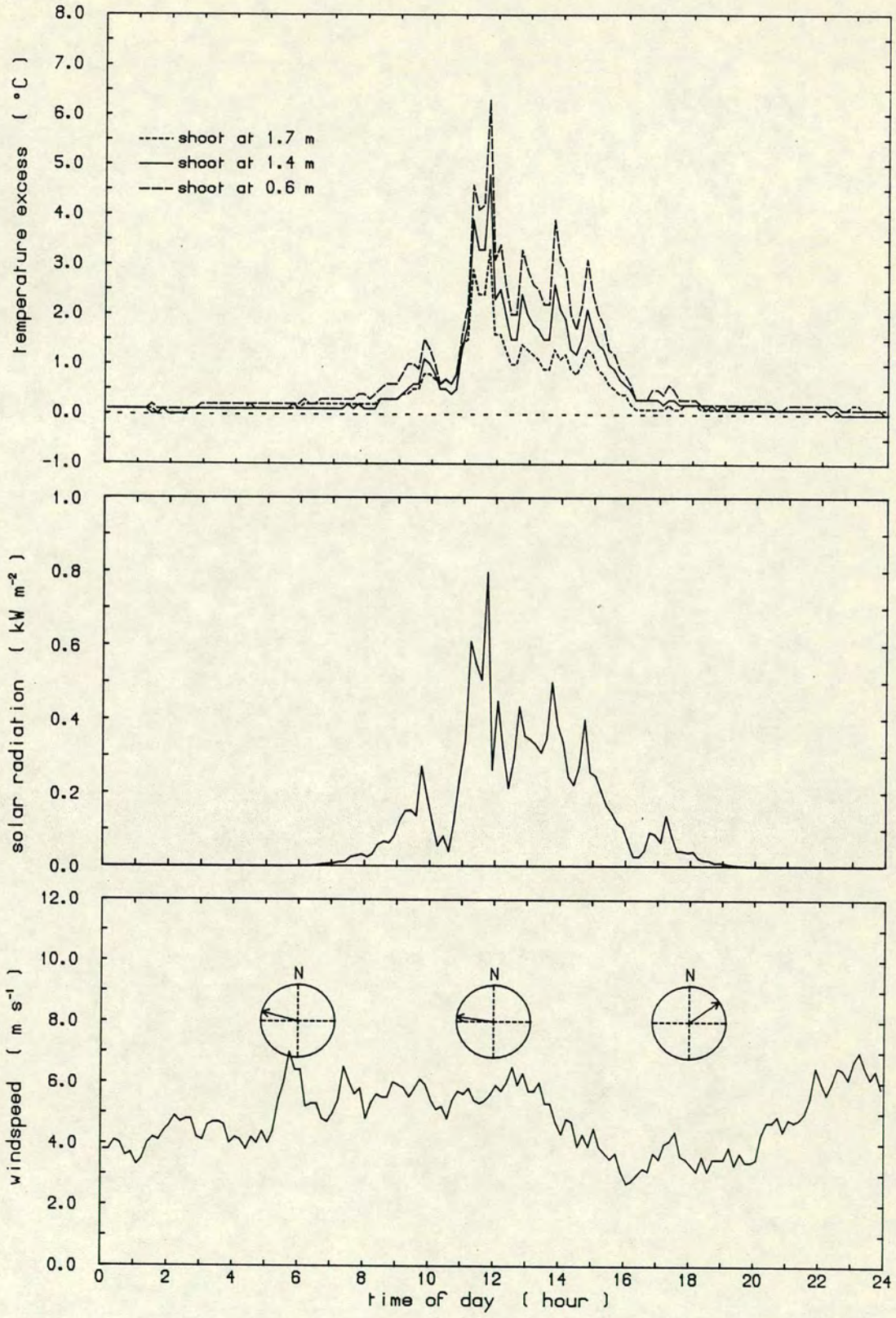


Figure 6.10. Temperature excesses on *Picea sitchensis* shoots at Dunslair Heights, 3 September 1984.

temperature differentials occurred. The most striking feature of the temperature data is the constant ranking of shoot temperature and height. The relationship is inverse, the lowest shoot always experiencing the greatest temperature excess, while the highest shoot is the coldest. The temperature of the shoot at the intermediate height is between those of the other two shoots. A further remarkable feature is the very clear coincidence between peaks of bud temperature and solar radiation.

On 6 September 1984 (figure 6.11) it was less windy, with a mean wind speed of 1.7 m s^{-1}, and rather sunnier, although the levels of solar radiation were still only moderate. Under these conditions, some very high bud-to-air temperature excesses were observed. The buds of the lowest shoot were nearly always warmer than those of the other shoots, achieving a maximum bud-to-air temperature differential of 8.1 °C. Again the ranking of temperature and height was very consistent, indicating the existence of a gradient of decreasing temperature with height.

6.3.2. Long-term temperature differences

The most straightforward way to investigate the long-term temperature differences between apices of differing exposure is to determine averages over long time periods. This has been done for each of the three series of measurements reported in this chapter. For each shoot studied, the apices' mean temperature excess above air and mean absolute temperature over the entire measuring period have been calculated. In addition, the standard deviations of these means have been determined, to give some idea of the variability in temperature. The results of these analyses are given in table 6.3.

The mean temperature excesses of the buds measured during September-October 1983 (table 6.3a) are all negative, indicating that the buds were mostly below air temperature. The mean excesses are very similar in value to one another. The shoot at 330° was the coolest, as would be expected from the prevailing wind direction, thought to be around 293° (see section 2.3). The standard deviations are also very similar, although there is a detectable trend toward increasing standard deviation with decreasing exposure. The standard deviation for the least exposed shoot is almost double that for the most exposed. This indicates that although the means are similar, the least exposed shoot more often experienced extreme temperature

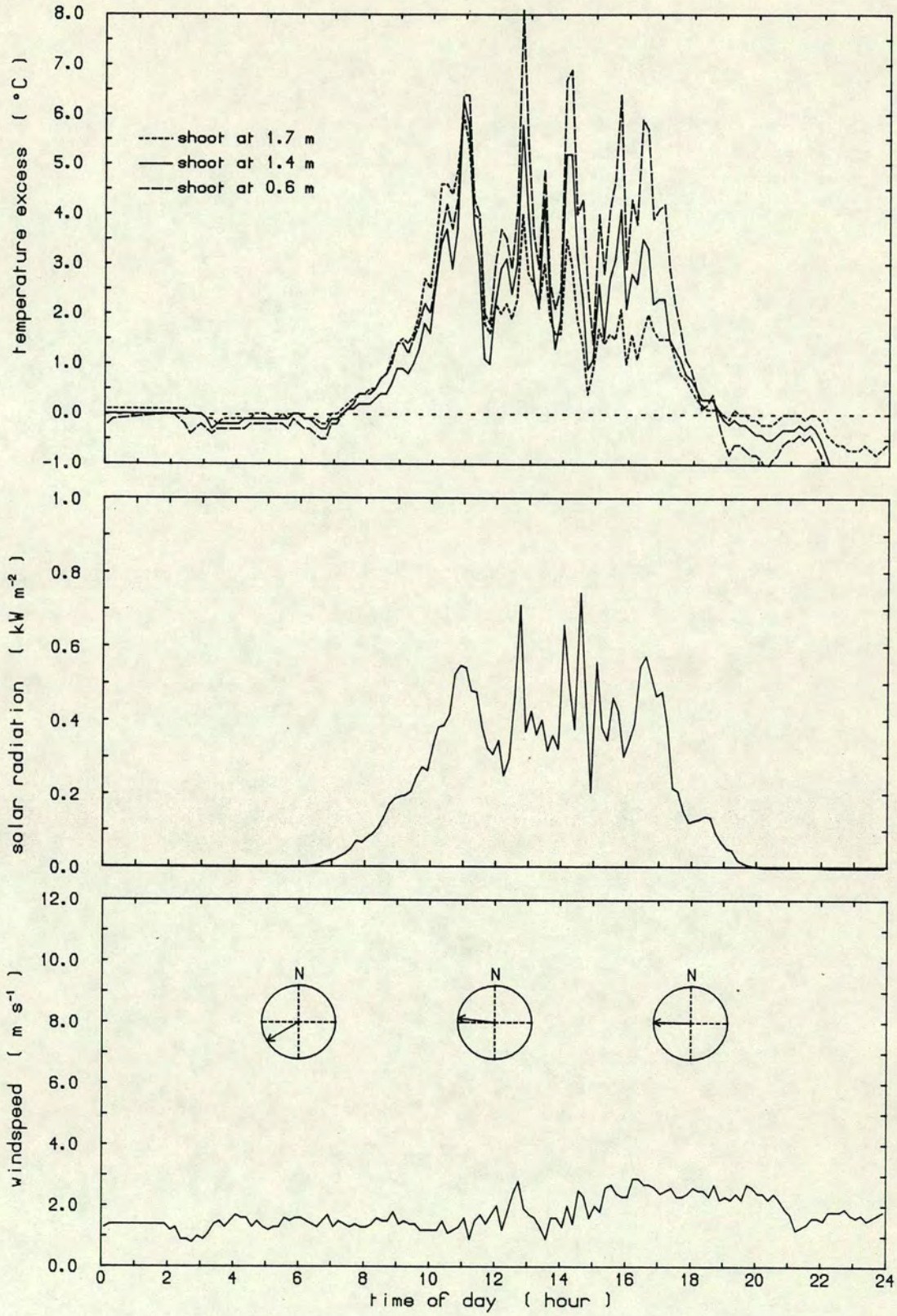


Figure 6.11. Temperature excesses on *Picea sitchensis* shoots at Dunslair Heights, 6 September 1984.

Table 6.3

Means and standard deviations of bud temperature measured at Dunslair Heights during 1983 and 1984.

(a) September to October 1983 (22 days' data)
Mean air temperature = 9.57 (standard deviation = 2.89)

Shoot angle (degrees)	Mean temperature excess (°C)	(S.D.)	Mean temperature (°C)	(S.D.)
330	-0.36	(0.33)	9,21	(2.84)
30	-0.18	(0.44)	9.38	(2.92)
120	-0.17	(0.62)	9.39	(2.80)
180	-0.17	(0.44)	9.40	(2.80)

(b) June to July 1984 (43 days' data)
Mean air temperature = 13.60 (standard deviation = 4.69)

Shoot angle (degrees)	Mean temperature excess (°C)	(S.D.)	Mean temperature (°C)	(S.D.)
295	0.31	(0.57)	13.91	(5.01)
33	0.15	(0.59)	13.75	(4.93)
108	0.21	(1.07)	13.82	(5.02)
202	0.33	(0.97)	13.93	(5.18)

(c) August to September 1984 (16 days' data)
Mean air temperature = 17.10 (standard deviation = 4.28)

Shoot exposure	Shoot height (m)	Mean temperature excess (°C)	(S.D.)	Mean temperature (°C)	(S.D.)
leeward	1.7	0.33	(1.23)	17.43	(4.30)
windward	1.2	0.60	(1.40)	17.70	(4.93)
leeward	1.4	0.64	(1.28)	17.74	(4.53)
leeward	0.6	1.02	(1.66)	18.12	(4.89)

excesses. The absolute temperature means are also almost the same. Only 0.2 °C separates the greatest from the least. The shoot thought to experience the greatest exposure to wind has the lowest mean temperature. There appears to be no trend in the standard deviations of absolute bud temperature.

The means and standard deviations for June-July 1984 are given in table 6.3b. The mean temperature excesses for the apices are positive, ranging from 0.15 °C to 0.33 °C. There is no clear relationship between mean apex-to-air temperature differential and a shoot's presumed degree of exposure. The shoot at 295°, i.e. facing almost directly towards the apparent prevailing wind direction, has the third highest mean, instead of the expected lowest. A similar trend in the standard deviations is observed as before. The lesser a shoot's presumed exposure, the greater the standard deviation of its apex-to-air temperature excess. The mean absolute temperatures are close in value, spanning a range of less than 0.2 °C. No obvious relationship between exposure and mean or standard deviation of absolute temperature can be detected.

Table 6.3c shows the summary statistics for the August-September 1984 period of data collection. The mean temperature excesses are positive and span a wider range (0.7 °C) than either of the cases presented above. The shoot at the greatest height of 1.7 m has the smallest mean excess (0.3 °C) and the lowest shoot, at a height of 0.6 m has the largest mean excess (1.0 °C). The ranking of the shoots' mean excesses shows a clearly inverse relationship between bud-to-air temperature differential and height. This reflects a probable increase in wind exposure with height. The mean absolute temperatures show the same clear relationship. There is no obvious pattern in the standard deviations of absolute bud temperature, despite a trend in the standard deviations of temperature excess toward an increase in value with a decrease in height.

Although means and standard deviations are simple and easily-calculated summary statistics, their use obscures most of the information present in the data. In order to reduce the data to a form which allows easy comparison of the temperatures of the various shoots, yet preserves more of the information, cumulative frequency distributions were calculated. These distributions give some idea of the frequency with which higher, growth-enhancing

temperatures were experienced by each shoot. For each series of field measurements, cumulative frequency distributions of apical temperature excess and absolute apical temperature were determined for each shoot studied. The distributions are presented below in graphical form.

Figure 6.12 shows the distributions calculated from the September-October 1983 series of measurements. For clarity, the distributions of bud temperature for the two shoots of intermediate exposure (as judged from the apparent prevailing wind direction) have been omitted from the diagrams. These distributions lay in between those of the most exposed shoot (shoot at 330°) and most sheltered shoot (120°). Inspection of the graph of the distributions of bud-to-air temperature differential (fig. 6.12a) shows that the sheltered shoot experienced a greater frequency of large differentials than the exposed shoot. Indeed, the exposed shoot never experienced a temperature excess greater than 1 °C, whereas the maximum for the sheltered shoot was 3 °C. The sheltered shoot also experienced a slightly higher frequency of the lower temperature excesses (< -1 °C) than the exposed shoot. These observations confirm the trend detected in the standard deviations of bud-to-air temperature differential. The distributions of absolute bud temperature (fig. 6.12b) are, however, very similar to one another. The line for the exposed shoot is almost always to the left of the line for the sheltered one, thus indicating that the exposed shoot was more frequently below any given temperature than the sheltered one, but the difference exhibited is small. The general magnitudes of bud temperature are rather low, ranging from 4 °C to 17 °C. This reflects the time of year and the poor (i.e. wet, windy and cloudy) weather conditions during the measurement period.

The cumulative frequency distributions for June-July 1984 are given in figure 6.13. As above, the distributions for the shoots of intermediate exposure have been omitted to improve clarity. The sheltered shoot (108°) experienced a greater frequency of high temperature excesses than the exposed shoot (295°). The exposed shoot was rarely more than 3 °C warmer than the air, whereas the sheltered achieved apex-to-air differentials greater than this (up to 5 °) about 4% of the time. Lower temperature excesses were also experienced more frequently by the sheltered shoot. Thus the sheltered shoot exhibits a greater variability in the apex-to-air temperature differentials experienced than the exposed shoot. This agrees with the above-noted trend in the standard

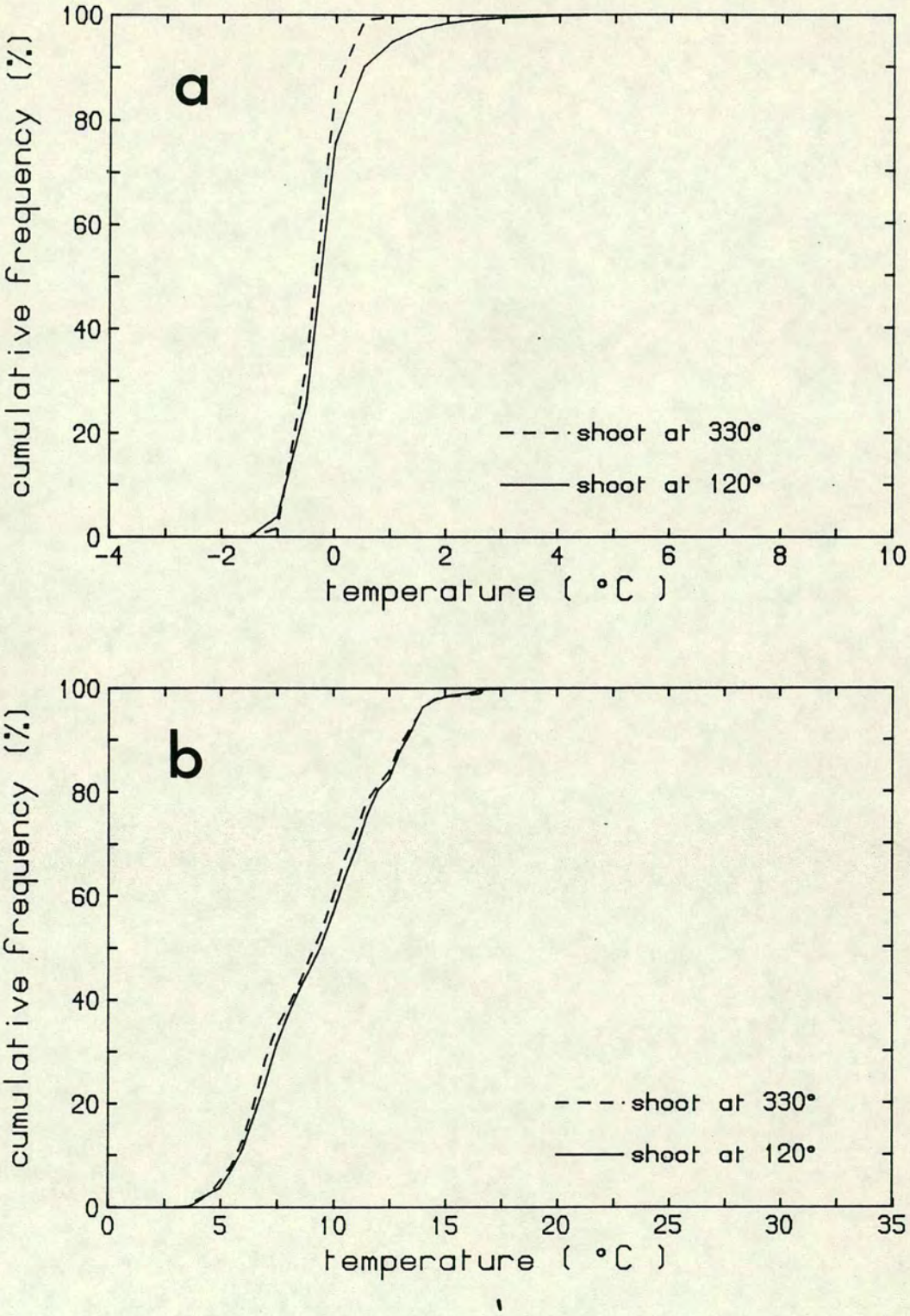


Figure 6.12. Cumulative frequency distributions of (a) excess temperature, and (b) absolute temperature, September - October 1983.

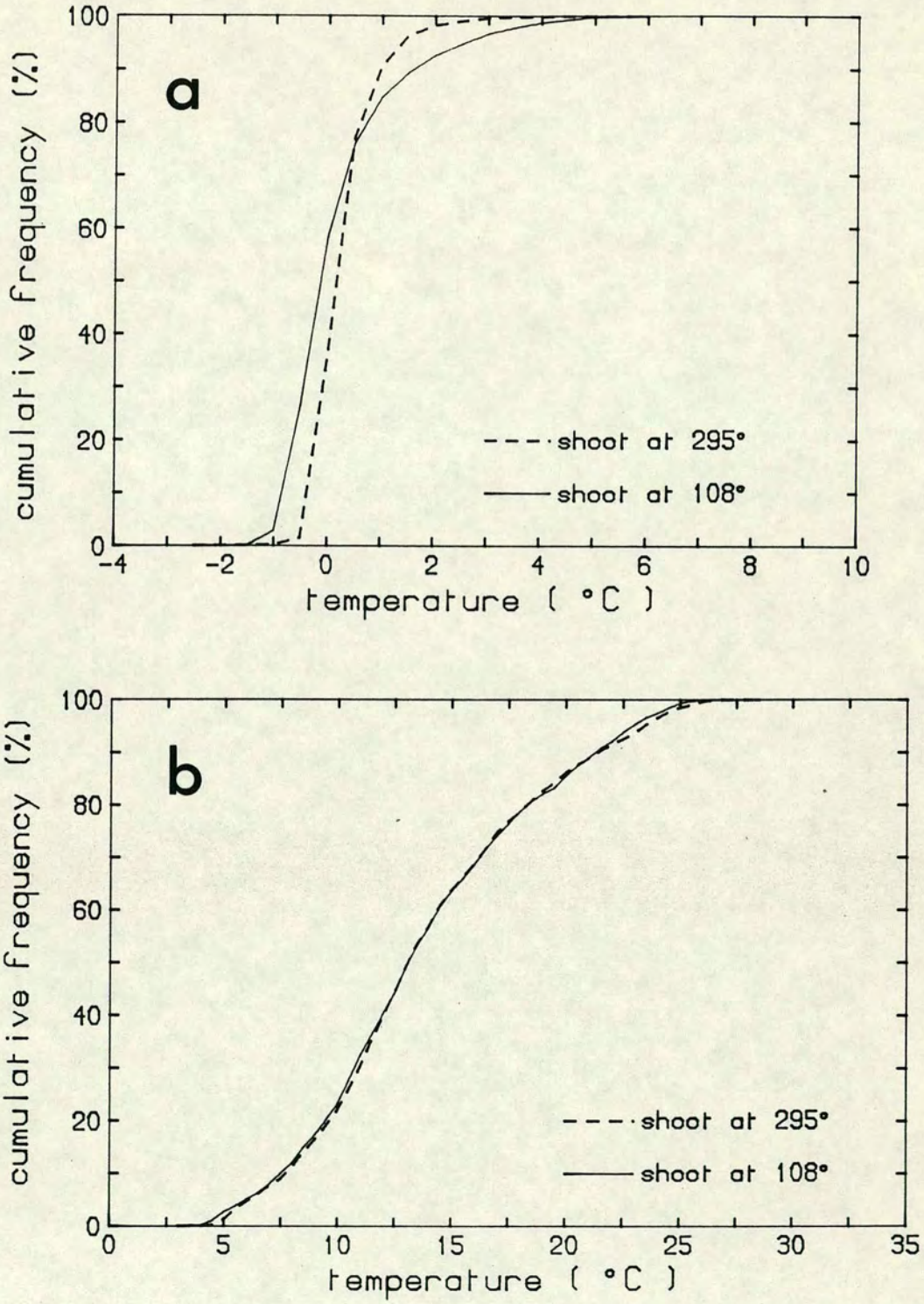


Figure 6.13. Cumulative frequency distributions of (a) excess temperature, and (b) absolute temperature, June - July 1984.

deviations. Reference to the graph of the distributions of absolute apical temperatures (fig. 6.13b) shows that there was hardly any difference in the temperatures of the two shoots. The range of temperatures experienced is broader than in September-October 1983, spanning 4 °C to 26 °C.

Much greater differences in the frequency distributions of temperature experienced by the various shoots were found during the August-September 1984 period of data collection (figure 6.14). The highest shoot, at 1.7 m, more often experienced low bud-to-air temperature excesses than the shoot at 1.4 m, which experienced small excesses more frequently than the lowest shoot, at 0.6 m (fig. 6.14a). The shoot at 0.6 m experienced bud-to-air differentials greater than 2 °C roughly twice as frequently as the shoot at 1.4 m, and four times as frequently as the highest shoot. This hierarchy is also evident when the cumulative frequency distributions of absolute bud temperatures are examined (fig. 6.14b). The lowest shoot was the only one to experience temperatures between 26 °C and 31 °C, which occured for 6% of the time. The lowest temperatures experienced by the shoots were more or less identical.

In an attempt to examine the maximum differences in temperature that might occur for shoots at different positions in a tree growing at a site where the wind always comes from the same direction, the data from September-October 1983 and June-July 1984 were re-analysed. Cumulative temperature distributions were determined for a sheltered and an exposed shoot using a 'dynamic definition' of exposure. This was achieved, using a computer program, as follows. For each ten-minute period of data, the 'exposed' shoot was defined as the one (of the four) closest to the current wind direction and the 'sheltered' shoot as the one most nearly pointing in the opposite direction. The temperatures and temperature excesses of these shoots were thus considered to represent those of the 'exposed' and 'sheltered' shoots of a tree in an imaginary environment of unvarying wind direction over that particular ten-minute period.

Figures 6.15 and 6.16 show the results of this analysis for September-October 1983 and June-July 1984 respectively. Over both time periods the distributions of absolute bud temperature are very similar, but a slight tendency for the 'sheltered' shoot to experience a greater frequency of

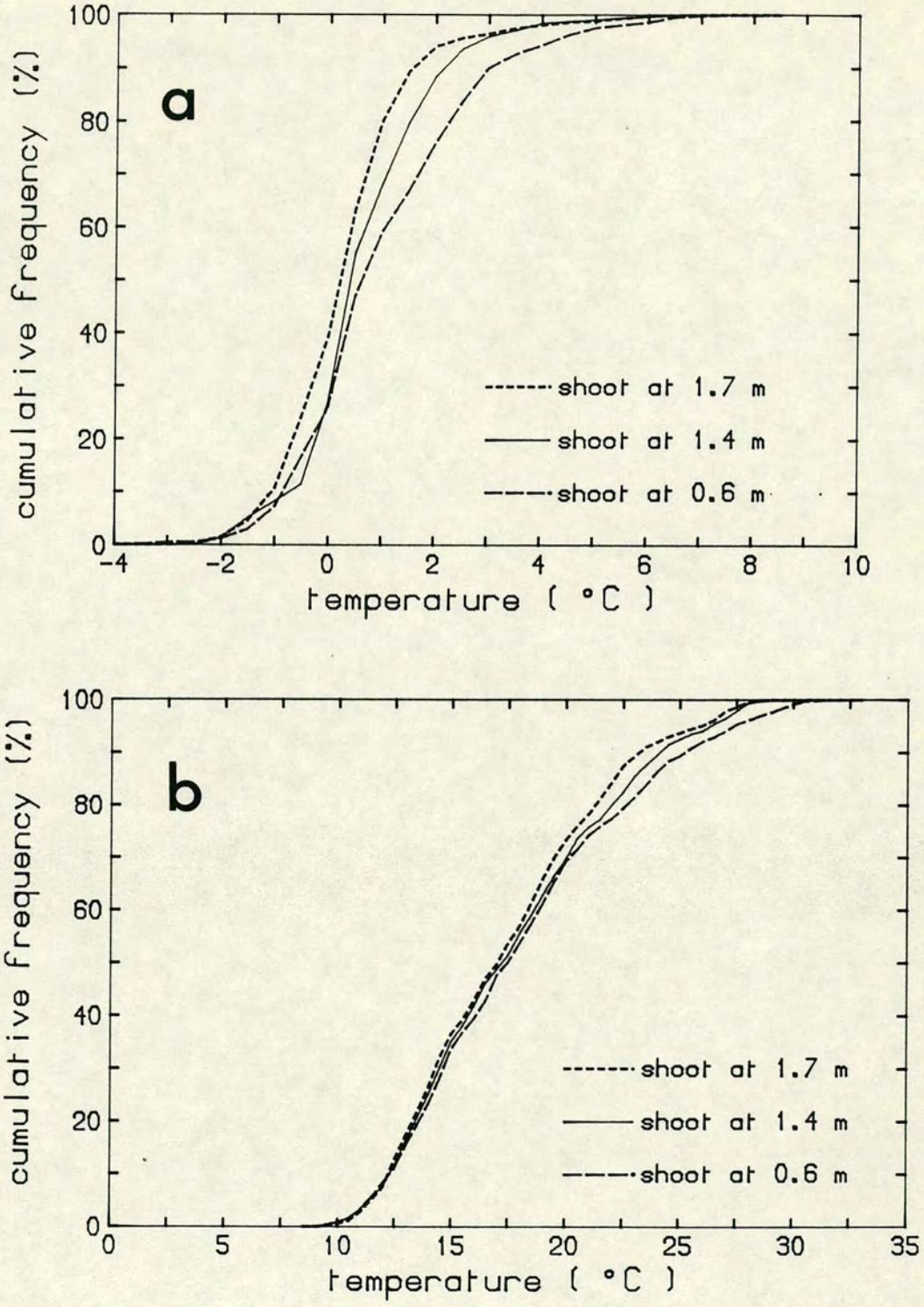


Figure 6.14. Cumulative frequency distributions of (a) excess temperature, and (b) absolute temperature, August - September 1984.

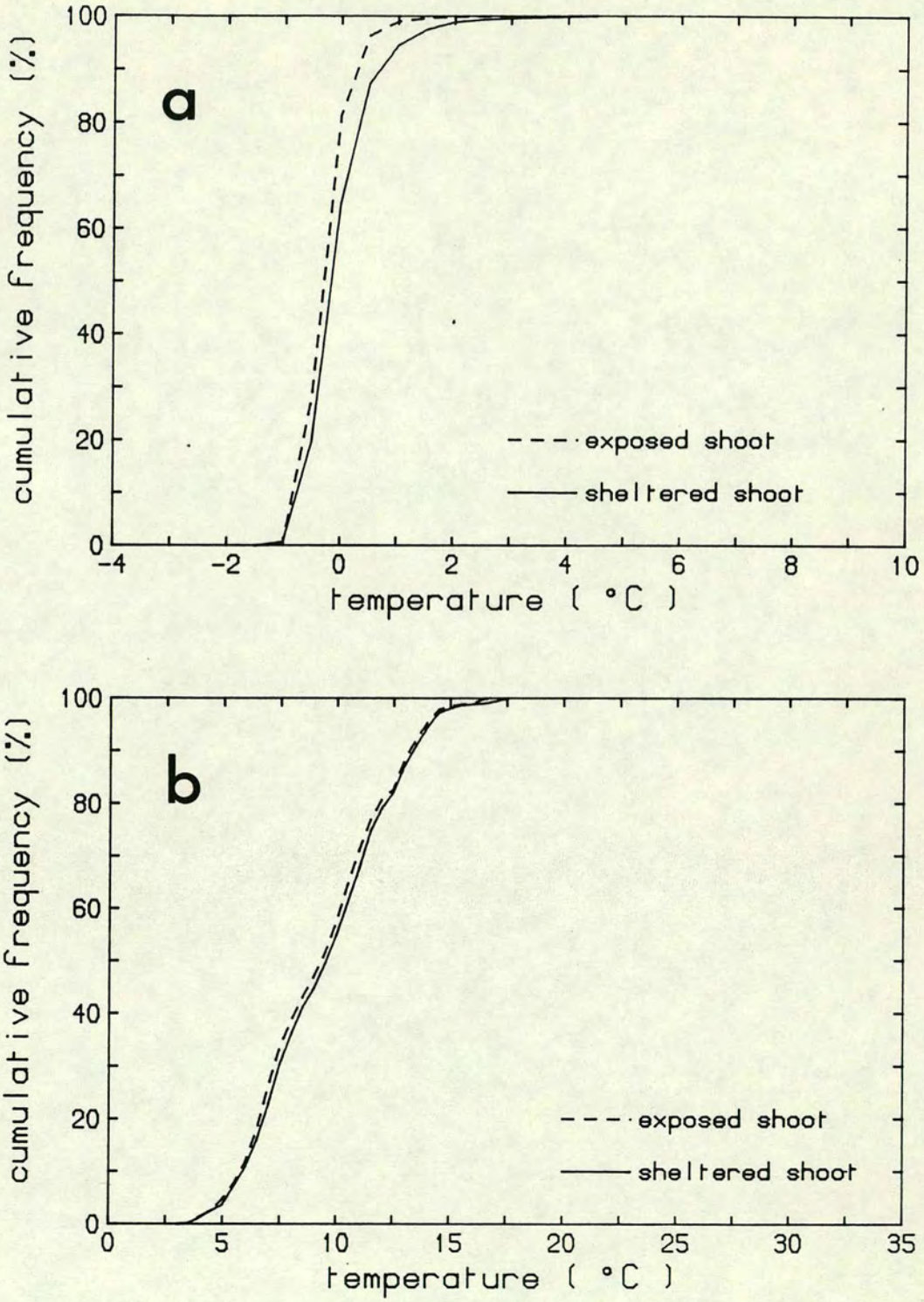


Figure 6.15. Cumulative frequency distributions using dynamic definition of which shoots are exposed and which are sheltered: (a) excess temperature, (b) absolute temperature. September - October 1983.

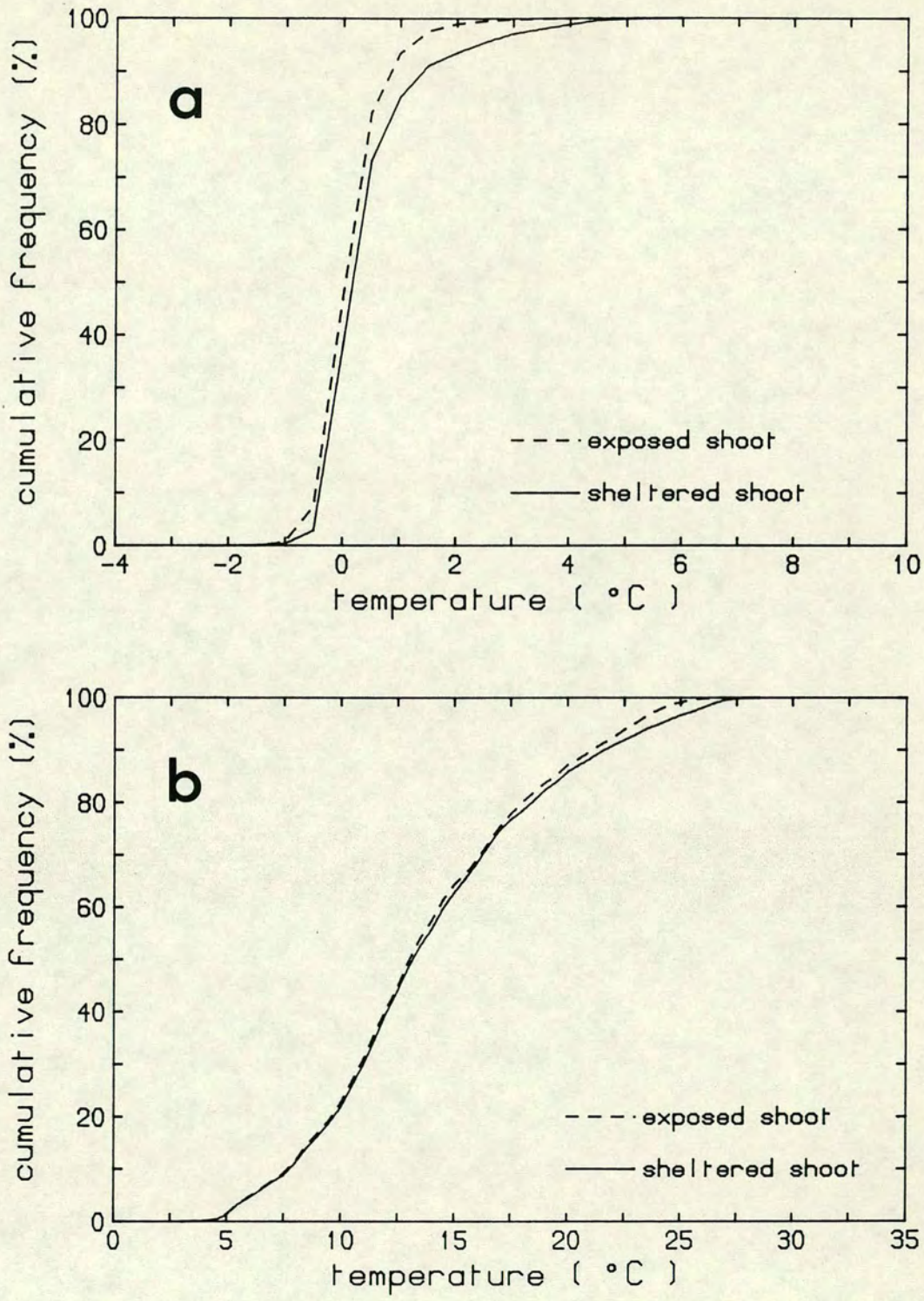


Figure 6.16. Cumulative frequency distributions using dynamic definition of which shoots are exposed and which are sheltered. (a) excess temperature, (b) absolute temperature. June - July 1984.

high temperatures is shown in the distributions based on the June–July data. The dynamic definition of shelter produced greater effects on the cumulative frequency distributions of apex-to-air temperature excess. For both sets of data, the 'sheltered' shoot still experiences large excesses more often than the 'exposed' one, but it no longer experiences negative excesses more frequently (compare with figures 6.12a and 6.13a).

6.3.3. Wind exposure and boundary layer resistance

The measurements obtained during the period June–July 1984 were subjected to an analysis designed to determine the relationship between windspeed (u) and the boundary layer resistance to heat transfer (r_a) for shoot apices of differing exposure to the wind. Only part of the large pool of data (sets of ten-minute averages of the quantities measured over 44 days) was included in the analysis. Two main selection criteria, based on wind direction and time of day, were used. The reason for their use is explained below.

The basic principle of the analysis is that r_a for an apex (assuming no water loss by evaporation) can be calculated, if a range of measured values of net radiation and corresponding apex-to-air temperature differentials are available.

The first difficulty is that the net radiation absorbed by the apex is required for the calculations. During June–July 1984, only the solar irradiance was measured. Fortunately, Miranda *et al* (1984) have made simultaneous measurements of solar and net radiation above a *Calluna vulgaris* -dominated heath, occupying a hilltop near the field site. They obtained the following, highly significant, linear regression of net radiation, **R**, against solar irradiance, **S** (95% confidence limits shown in brackets):

$$\mathbf{R} = 0.74\ (\pm 0.02)\ \mathbf{S} - 7\ (\pm 10)$$

On the assumption of similarity between the radiation exchanges of spruce and heather foliage, the above regression was used to convert the measured values of solar irradiance to net radiation.

A further problem arises from the differences in the surface geometries of

the shoot apex (which is roughly cylindrical and surrounded by needles) and the radiation sensor (which is a horizontal plane). As discussed previously (section 5.4) the reading of the radiation sensor does not necessarily correspond accurately with the amount of net radiation absorbed by the apex. Serious under-estimation of the net radiation absorbed by the apex is likely to occur early in the morning and late in the afternoon, when the sun is close to the horizon. However, when the sun is near its zenith, it is likely that the error will be small. Bearing this in mind, data collected before 10:00 and after 16:00 (BST) were arbitrarily omitted from the analysis.

The objective of the analysis was to examine the effect of the degree of shelter experienced by a shoot on the relationship between the boundary layer resistance of its apex and wind speed. This requires that each shoot studied should have experienced a constant degree of wind exposure during the period of measurements. Wind direction was, however, not constant. The shoot that was usually the most exposed was sometimes the most sheltered and *vice versa* (depending upon wind direction), thus confounding the analysis. To avoid this problem, only the data collected during periods when the wind was close to the prevailing direction were included in the analysis. The exact selection criterion used was that the wind direction lay between 270° and 320°. This selection procedure ensured that the relationship between r_a and u, obtained for each shoot, was indeed indicative of a particular degree of exposure.

Inspection of equation 5.5 shows that if a graph of apex-to-air temperature differential ($T_s - T_a$) values versus net radiation (**R**) readings is plotted, the slope of a straight line drawn to fit the points is equal to $r_a / (\rho C_p)$. The value of C_p is a constant (1010 J kg^{-1} $°C^{-1}$), and although the value of ρ is slightly dependent on temperature and humidity, it can also be considered constant (at 20 °C, for dry air, ρ = 1.204 kg m^{-3} (Monteith, 1973)), so r_a can be calculated.

Boundary layer resistance does not, however, have a constant value which is characteristic of the apex of a particular shoot. Rather, its value is dependent on wind speed (equation 5.6). Thus the value of r_a should only be calculated over a particular, narrow range of wind speed, by including only those values of $T_s - T_a$ and **R** that were measured when the wind speed was within that range. The variation of r_a with wind speed can thus be studied by

plotting several graphs of T_s-T_a versus **R** for each shoot and calculating a value of r_a for each different range of wind speed, or wind speed 'class'. For this analysis the data were put into groups, according to the following wind speed classes:

class 1: $0.0 < u < 1.0$ m s^{-1} (N = 4)
class 2: $1.0 < u < 2.0$ m s^{-1} (N = 66)
class 3: $2.0 < u < 3.0$ m s^{-1} (N = 171)
class 4: $3.0 < u < 4.0$ m s^{-1} (N = 150)
class 5: $4.0 < u < 6.0$ m s^{-1} (N = 215)
class 6: $6.0 < u < 8.0$ m s^{-1} (N = 136)
class 7: $8.0 < u < 10.0$ m s^{-1} (N = 99)

The wind speed only fell into class 1 on four occasions, providing a sample of measurements which was too small to be included in the analysis, on statistical grounds.

A graph of T_s-T_a against **R** was plotted for each wind speed class (2-7), for each shoot, producing a total of 24 graphs. A selection of these is reproduced to show the nature of the data. Each figure presented shows data collected when the wind speed was in one of the classes, defined above (figure 6.17 - class 2, figure 6.18 - class 4, figure 6.19 - class 5, figure 6.20 - class 6). The top graph (a) in each figure shows data for the most exposed shoot (295°), and the bottom graph (b) shows data for the most sheltered shoot (108°).

A linear regression was calculated to fit the scatter of points on each of the 24 graphs. The slopes of these regressions were used to calculate values for r_a. The regression lines obtained are shown on the graphs presented in figures 6.17 to 6.20. It is worth noting some features of these figures.

Firstly, for any particular wind speed class the slope of the regression for the exposed shoot is always less than that for the sheltered shoot, i.e. $r_a^{ex} < r_a^{sh}$ (c.f. equation 5.8).

Secondly, the higher the wind speed class, the lower the boundary layer resistance for the apex of either shoot. There is clearly an inverse relationship between wind speed and boundary layer resistance.

These observations are confirmed by figure 6.21, which is a summary of

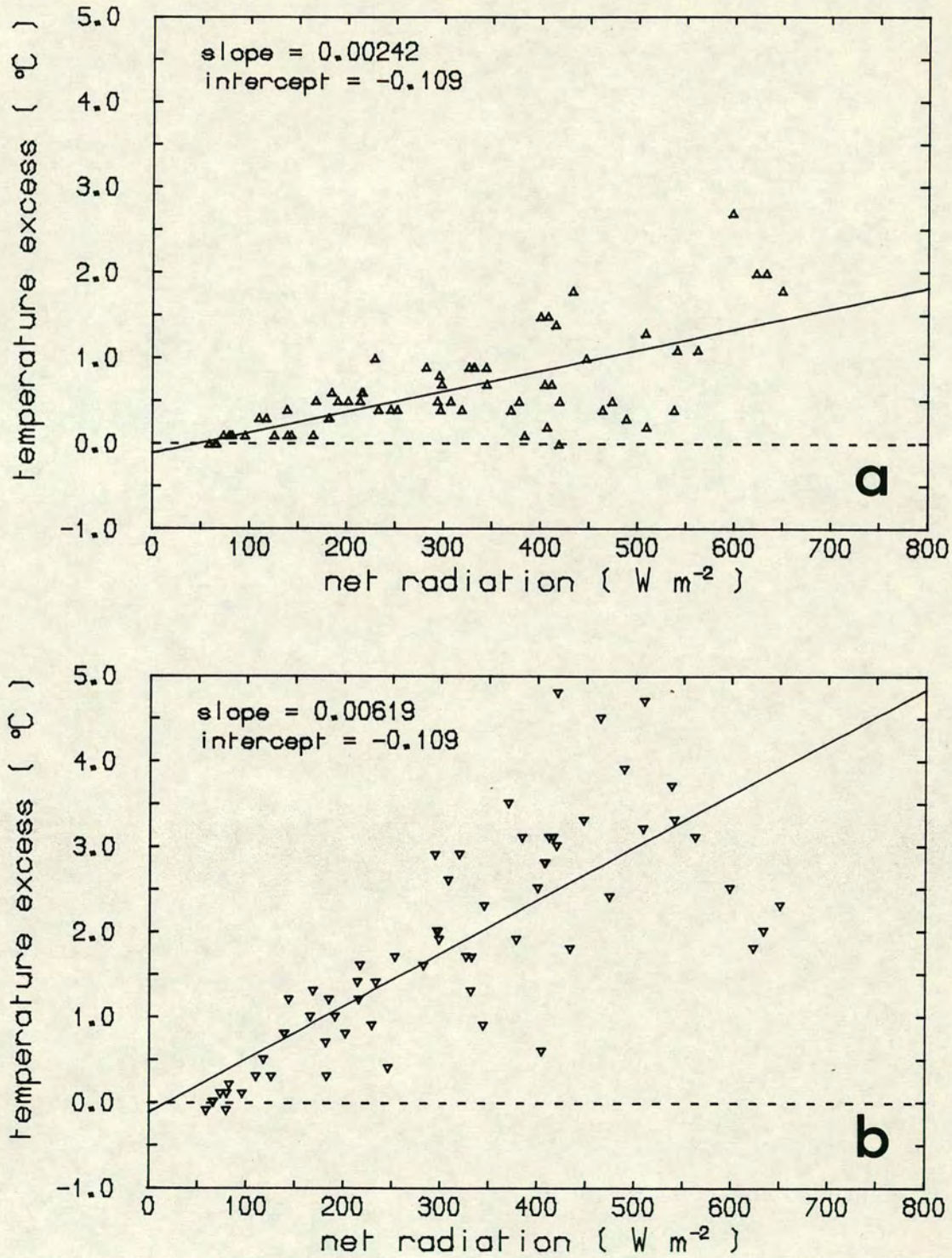


Figure 6.17. Temperature excess plotted against net radiation, using data collected in windspeed range 1.00 - 1.99 m s^{-1}. Figure (a), exposed shoots, Figure (b), sheltered shoots. N = 66.

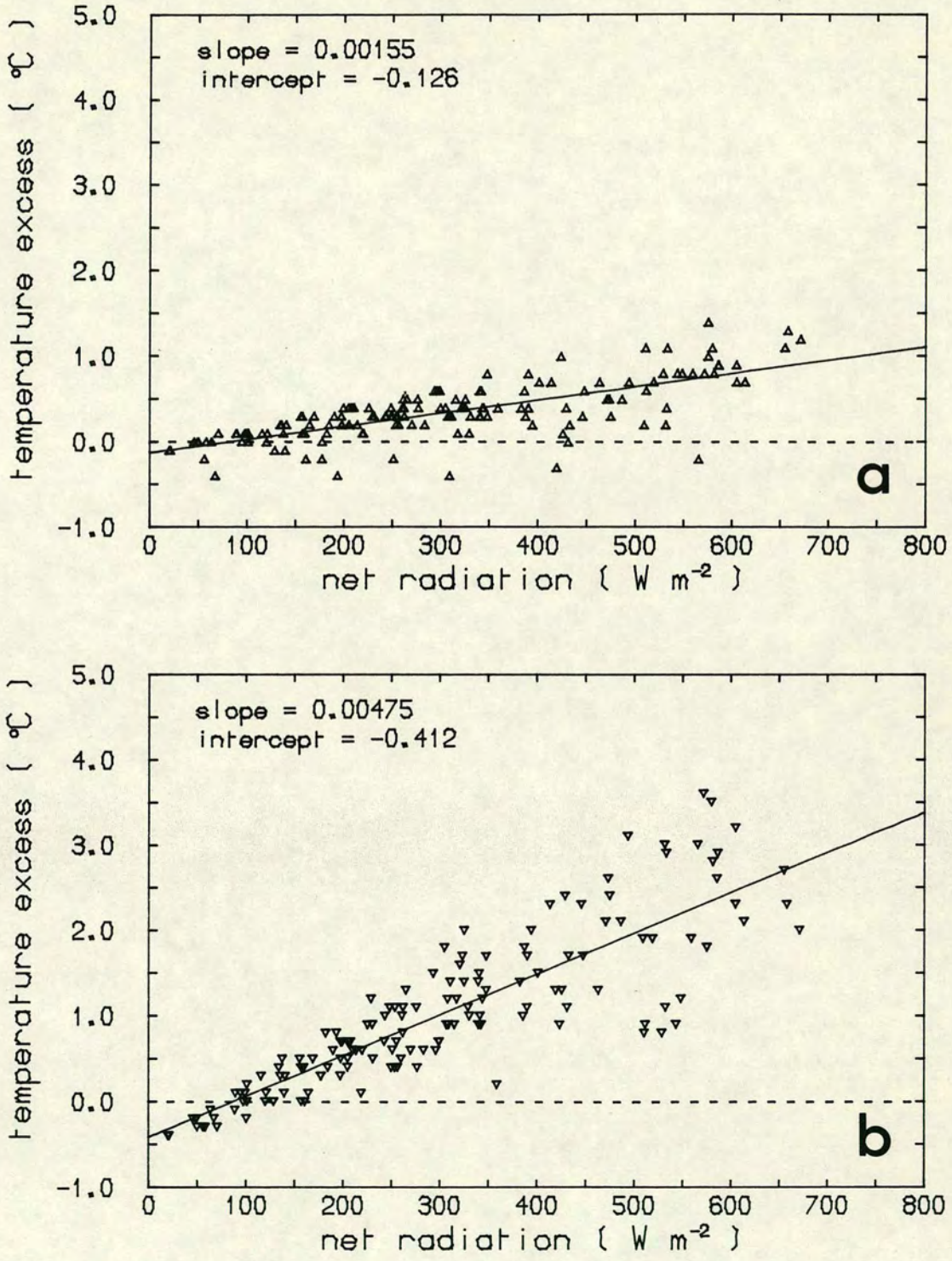


Figure 6.18. Temperature excess plotted against net radiation, using data collected in windspeed range 3.00 - 3.99 m s^{-1}. Figure (a), exposed shoots, Figure (b), sheltered shoots. N = 150.

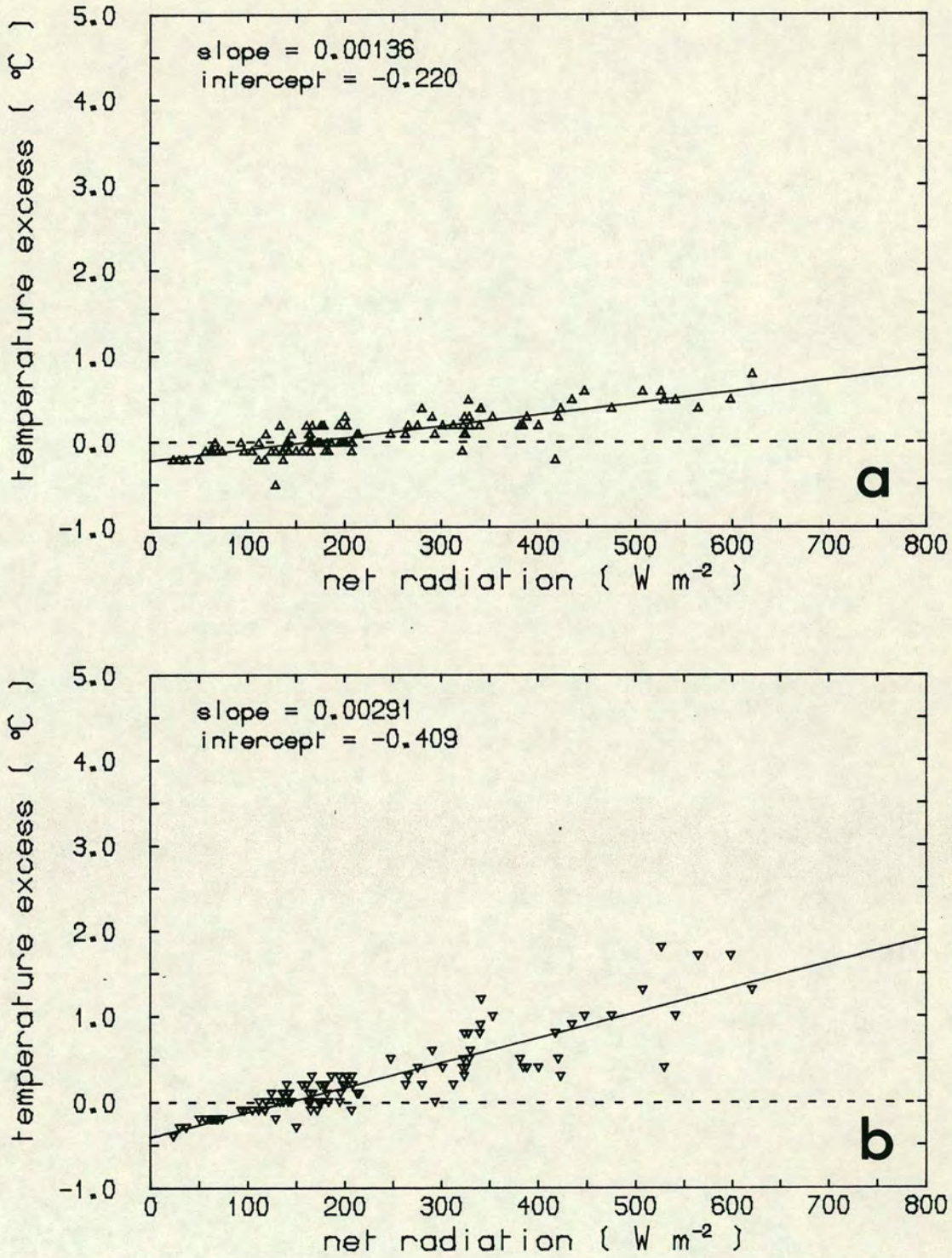


Figure 6.19. Temperature excess plotted against net radiation, using data collected in windspeed range 5.00 - 5.99 m s^{-1}. Figure (a), exposed shoots, Figure (b), sheltered shoots. N = 101.

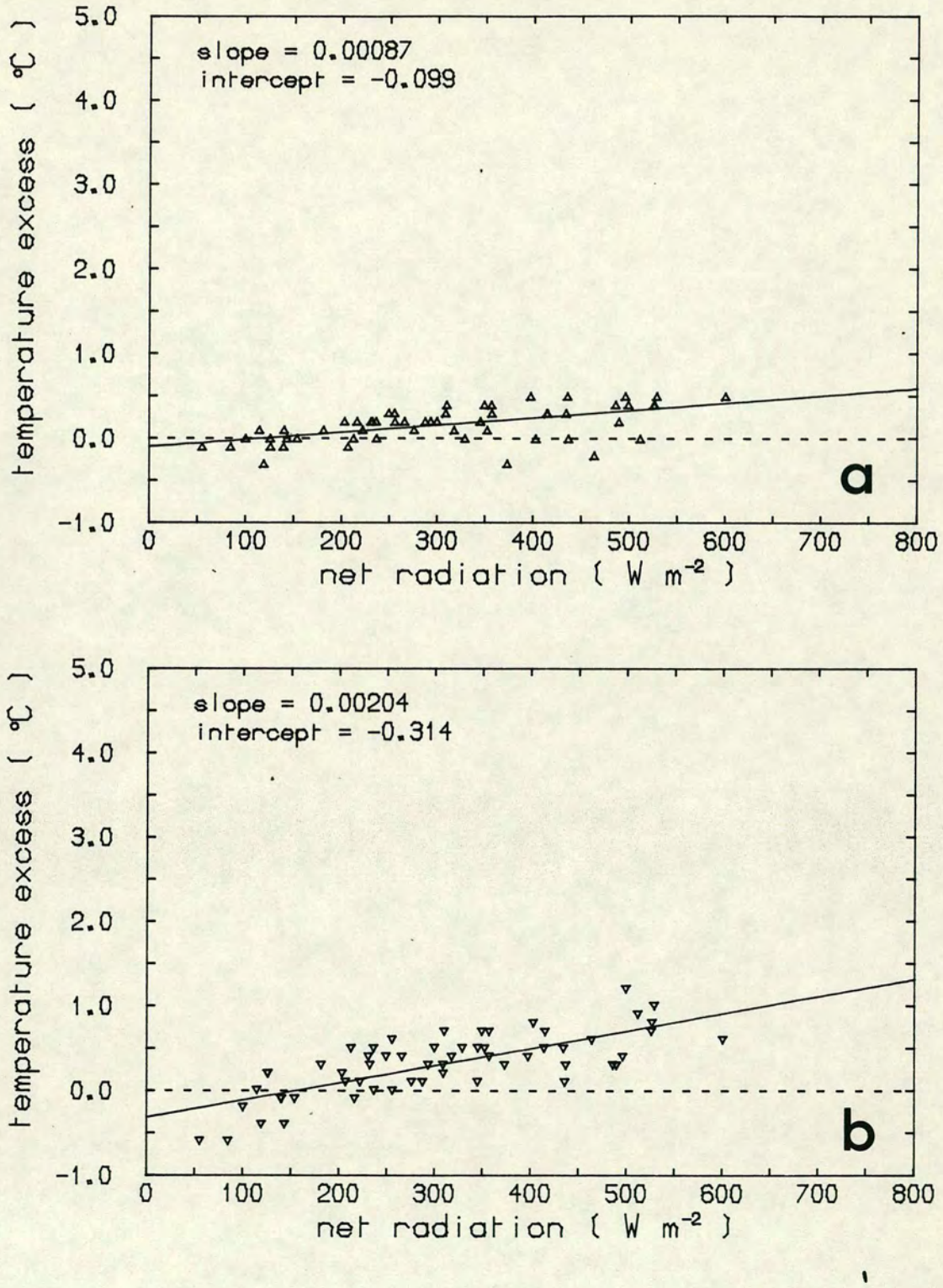


Figure 6.20. Temperature excess plotted against net radiation, using data collected in windspeed range 7.00 - 7.99 m s^{-1}. Figure (a), exposed shoots, Figure (b), sheltered shoots. N = 58.

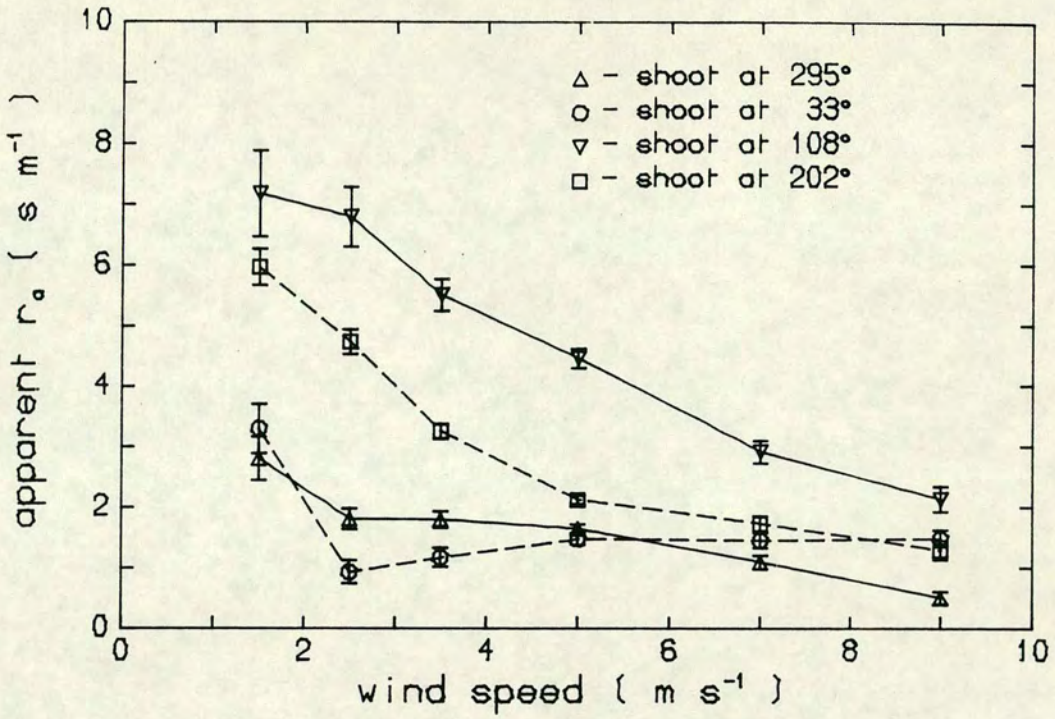


Figure 6.21. Apparent aerodynamic resistance plotted against windspeed for shoots of various orientations. The most sheltered situation was 108°.

the entire analysis. It graphically depicts the relationship between the boundary layer resistance of the apex of each shoot and wind speed (values of r_a are plotted against wind class mid-point). It can be seen that the resistance for the most sheltered shoot (108°) is always greater than the resistances of the other shoots, at all wind speeds. The lowest resistances are exhibited by the most exposed shoot (295°) and one of the shoots of intermediate exposure (shoot at 33°). The general trend shown is declining resistance with increasing wind speed, the trend being most pronounced for the most sheltered shoot. A deviation from this pattern is shown by the shoot at 33°, whose resistance declines rapidly over the wind speed range of 1 to 3 m s^{-1}, then climbs very gradually as wind speed increases.

6.4. Discussion

The graphs presented in figures 6.4 to 6.11 show that the behaviour of the apex-to-air temperature differentials, with respect to the values of radiation and wind speed, agrees with the predictions of the energy balance theory discussed in section 5.1.1.

The magnitudes of the observed apex-to-air excesses are strongly dependent on the level of net radiation, as would be expected from equation 5.5. The highest excesses only occurred on sunny days such as 4 July (figure 6.8), 5 July (figure 6.7) and 24 July (figure 6.9). On overcast days, when the levels of net radiation were low, the temperature excesses were small (e.g. 13 July, shown in figure 6.6) or close to zero (e.g. 17 July, shown in figure 6.4).

The effect of wind speed is also clearly evident. Equation 5.5 predicts that at high wind speeds, which cause a reduction in boundary layer resistance, the apex-to-air temperature differentials will be diminished. This is strikingly shown by the data obtained on 25 June (figure 6.5), when the levels of net radiation were fairly high, but very strong winds kept the temperatures of the apices close to air temperature.

The theoretical argument for the existence of temperature differences across tree crowns hinges on the effect of the shelter provided by the foliage, on the temperature of the leeward shoot apex. The retardation of the wind as it passes through the crown, supposedly causes an increase in the boundary

layer resistance of the leeward shoot's apex, which thus experiences higher temperatures than the exposed shoot's apex. The data presented clearly show a positive correlation between shelter and apical temperature excess, therefore supporting this idea. On any of the days presented from the June–July 1984 period of data collection, when the temperatures of four shoots of different orientation within the same whorl were measured, the greatest temperature excess was almost always experienced by the shoot pointing away from the wind (i.e. the most sheltered shoot). The dependence of apical temperature excess on the degree of shelter was shown particularly well by the measurements made on 24 July (figure 6.9). Different shoots were the warmest at different times, according to the direction of the wind, which veered rapidly throughout the day. At any particular time, it was always the leeward shoot that was warmest.

Shelter is probably the most important causative factor of the strong inverse relationship between shoot height and temperature that was observed during August–September 1984. The highest shoot measured, although on the 'sheltered' side of the tree (with respect to prevailing wind direction), actually benefitted from very little shelter. It was situated in the one-year-old whorl, where there is not much foliage to provide shelter, so that it probably experienced almost as much exposure to the wind as the 'exposed' shoot of the whorl. The lowest shoot, on the other hand, belonged to the nine-year-old whorl, quite close to the base of the tree. Here there was a great deal of foliage to protect it from the wind incident upon the sheltered side of the tree. This is likely to be one of the main reasons why the lowest shoot was nearly always warmer than the highest one.

Other factors, however, are involved. It is well known that there is a profile of declining wind speed close to the ground (Geiger, 1966). This arises from retardation of the airflow, by frictional forces, as it passes over the ground surface. This, by itself, would tend to favour higher temperatures near the base of the tree, as the lowermost shoots will possess the greatest boundary layer resistance. Warren Wilson (1959), measured the vertical variation in shoot temperature excess of a branch of *Salix arctica* held in a vertical position. He found that the temperature excess decreased from 4 °C close to the ground to less than 2 °C at a height of 0.25 m. Over the same vertical range, wind speed increased from 0.5 m s^{-1} to 2.5 m s^{-1}. Thus the lower shoots of the spruce

trees benefit from both lower wind speed and greater amounts of foliage to afford shelter.

In addition to the vertical profile of wind speed, there is also known to be a profile of air temperature, the air close to the ground being warmer than that above it (Geiger, 1966). During the study under discussion, air temperature was only measured at a height of 1.7 m. Thus it is possible that an undefined fraction of the higher values of apex-to-air differentials observed for the lowest shoot could have arisen from it being surrounded by air that was warmer than the air whose temperature was being recorded. If this were the case, the real increase in apical temperature excess with declining height would have been less than apparent from the measurements. This possibility is, however, rejected. Considering the high wind speeds prevalent at the field site and the aerodynamic roughness of an open spruce plantation, the airflow would have been too turbulent to permit the development of a significant difference between the air temperatures at 0.6 m and 1.7 m (the heights of the lowest shoot studied and the air temperature sensor). Miranda (1982), who studied temperature profiles over an aerodynamically less rough heather moorland, rarely measured temperature differences of more than 0.5 °C over a similar height interval.

During the June-July 1984 measurement period several days occurred when it was very sunny and the wind speed was low. Under these conditions, which would be expected to produce maximal apex-to-air temperature excesses, the apices never achieved temperatures more than 6 °C above the air temperature. On 28 September 1982, the bud-to-air temperature differential for the sheltered shoot of an Arolla pine attained peak values between 6 °C and 7 ° on several occasions. Although the wind speed was low on this day, the amount of net radiation was only moderate. This implies that under conditions of full sunlight and low wind speed the bud-to-air temperature differential of the Arolla pine's sheltered shoot might have been considerably greater. It does not seem unreasonable to suggest that a temperature excesses of perhaps 10 °C might sometimes be achieved, especially if the observation, by Tranquillini and Turner (1961), of a maximum excess of 21.5 °C for an Arolla pine shoot is brought into consideration.

Several explanations are possible for the apparent tendency of Sitka spruce

shoots to experience lesser temperature excess than Arolla pine shoots.

Firstly, there is an obvious difference in shoot morphology. The Arolla pine has long needles, which are densely packed around the bud. In Sitka spruce the needles are much shorter and much more sparsely distributed, affording little shelter to the shoot apex. Thus, the characteristic dimension (d in equation 5.6) for a Sitka spruce shoot apex is less than that for an Arolla pine. This means that the boundary layer resistance of the Arolla pine apex will be greater, reducing the rate at which it can dissipate heat by convective heat transfer and so causing it to experience higher temperatures.

Secondly, the whorl of Sitka spruce shoots measured during June-July 1984 was at a height of 1.7 m, over 1 m higher from the ground surface than the 'exposed' or 'sheltered' Arolla pine shoots. Thus, they probably experienced greater ambient wind speeds, because of the vertical gradient in wind velocity.

The third possible explanation is that there was more evaporative water loss from the apices of the extending Sitka spruce shoots than from the Arolla pine buds. This seems likely to be true to some extent. The Arolla pine buds were covered in overlapping, resinous scales, whereas the Sitka spruce apices had only a newly-developed cuticle to prevent evaporation. Measurements of evaporation rates are required to evaluate the significance of the differences between these two surfaces.

In order to allow assessment of the significance for asymmetrical growth of temperature differences between shoots, the means and cumulative frequency distributions of shoot excess and absolute temperature for each measurement period, have been presented. Firstly, the results of these analyses for the first two periods of data collection (September-October 1983 and June-July 1984), when shoots at the same height and different orientations were compared, will be discussed. Subsequently, the results of these analyses on the data obtained during August-September 1984, when the vertical variation of shoot temperature was studied, will be examined.

The means for both September-October 1983 and June-July 1984 show very little difference between the temperatures of the apices of the different shoots. The temperatures experienced by the shoots are so similar that it is hard to imagine asymmetrical growth occuring as a result of temperature

differences, if growth is presumed to respond linearly to temperature. The cumulative frequency distributions show that sheltered shoots tend to experience large temperature excesses more often than exposed ones. This apparent difference is found to be small when the distributions for absolute temperatures are calculated. Partly this is an effect of scale; when compared to air temperature the usual temperature excesses are rather small, only increasing shoot temperature a few percent above air. Partly, it results from the way the air temperatures and apex-to-air differentials sum to give the shoot temperatures. The naive assumption would be that large excesses always accompany high air temperature, thus sometimes allowing the sheltered shoot to become much warmer than any of the other shoots ever do. In reality, there appears to be no correlation between high air temperatures and large temperature excesses, so when viewed on a long-term basis the latter cause little difference in absolute temperature between the shoots of differing exposure.

The story is slightly different when the means for the August-September 1984 period are examined. The differences between the means are larger, possibly great enough to support enhanced growth of the lowermost shoot. The weather during the period of data collection was not particularly warm. If the same measurements were made in the fine, warm mid-summer period, even greater differences would probably be observed. It is interesting to note that annual shoot extension is much more asymmetrical near the bottom of the spruce trees, than near the apex, where the extensions achieved on the exposed and sheltered sides are very similar (see chapter 4 where some extension measurements are reported).

The general shape of the relationships obtained between boundary layer resistance and wind speed for the four shoots of differing exposure is in general agreement with theory. A quantitative relationship between r_a and wind speed can be calculated, for an object of a particular size and shape, from semi-empirical relationships that have previously been determined from rates of heat transfer in wind tunnel experiments. However, such relationships have been established only for relatively simple objects that are of interest to engineers, such as plates, spheres, cylinders and the inside of tubes (see Kreith, 1973). Attempts to apply these relationships even to simple biological objects, such as leaves, have often been unsuccessful (Grace and Wilson,

1976).

The principal reason for this difficulty is the aerodynamic complexity of plant parts. The apices of conifers are especially complex, not only as a result of the needles that surround them (Landsberg and Thom, 1971; Landsberg and Powell, 1973; Wilson and Crowther, 1985) but also because of the interference to the airflow caused by neighbouring branches and leaves. In the present study a further difficulty arises from the methodology employed; the rate of energy absorbed by the apices has been assumed to be equal to the net radiation absorbed by the vegetation as a whole.

Despite these difficulties the relationships between r_a and wind speed depicted in figure 6.21 are broadly similar in form to those reported before (Landsberg and Ludlow, 1970). The magnitudes of r_a are about half those reported by Landsberg and Ludlow (1970), who worked on water loss from whole shoots of Sitka spruce covered with gypsum.

The important conclusion from the graph is, however, that the apices of the shoots on the sheltered side of the tree have boundary layer resistances which are two or three times greater than for those on the exposed side. Thus the shelter afforded by the tree crown appears to be appreciable. The graph shows that the sheltered shoot apex had the same boundary layer resistance when the ambient wind speed was 8 m s^{-1} as the exposed shoot had when the ambient wind speed was 1 m s^{-1}, clearly illustrating the degree of shelter experienced by the leeward shoot. As a result of this shelter, afforded by the tree's foliage, the leeward shoots are generally warmer than the exposed ones, especially when the net radiation flux is high.

CHAPTER 7

EXPERIMENTAL INVESTIGATION OF THE EFFECT OF A TEMPERATURE GRADIENT ON SHOOT GROWTH

7.1. Introduction

Some field measurements of the temperature differences between shoot apices on the exposed and sheltered sides of trees have been reported above, in chapters 5 and 6 (for Arolla pine and Sitka spruce respectively). Fairly large temperature differences (up to 5 °C) were quite often recorded, the windward shoot being warmer than the leeward shoot, on almost all occasions.

It has been suggested that the occurrence of such temperature differences might account for the observed asymmetrical growth of wind-shaped trees (chapter 1 and section 5.1). The fact that temperature differences do exist, however, does nothing to prove that the greater warmth experienced by the sheltered side of a tree is actually responsible for the enhancement of its growth. Other wind-influenced processes could be the main causative agents and the temperature differences might have no real effect on growth.

This chapter reports an experiment that was performed in an attempt to rule out this possibility. Potted trees were grown in a greenhouse, in the absence of wind, and a thermal gradient was applied artificially. The growth of selected shoots was monitored through one growing season.

The species chosen for study were Sitka spruce and Scots pine (*Pinus sylvestris*). Arolla pines were not available, so Scots pine was used as a substitute. The results of the experimental treatment are not reported for Sitka spruce. This species was adversely affected by the temperature regime applied, producing two flushes of shoots of abnormal appearance, suggesting that any attempt to relate the experimental results to growth in an outdoor situation would be invalid.

7.2. Plant material

The plants used in the experiment were three Scots pine (Forestry Commission provenance NT11), aged four years (from seed), and four Sitka spruce (Queen Charlotte Island provenance), aged five years (from seed). These were selected for their good form and vigour from a larger group that had spent the previous winter in pots (15 cm diameter, 12 cm deep), standing outdoors on gravel, in the shelter of a wall. Shortly before the experiment the trees were transferred to larger pots (22 cm diameter, 22 cm deep), taking care not to disturb the ball of roots; University of California mix D2 compost was used. At this time, the trees were moved into the greenhouse and the experimental treatment was started. Bud break had not occurred, although the buds were no longer dormant, having begun to enlarge. No nutrient additions were made during the experiment. The trees were kept well-watered.

7.3. Methods

One side of each tree was cooled and the opposite side heated, so that a temperature difference existed between the two sides. This was achieved by standing the trees in a line between two parallel, vertical surfaces, one cooled and the other heated (plate 7.1). Both surfaces were painted white to minimise the effect of short-wave solar radiation on their temperature, it being particularly desirable to avoid heating of the cooled radiator by the sun. The long-wave emissivity of white paint is close to unity, so its use did not diminish the radiative coupling between the shoots and the two controlled temperature surfaces.

The heated surface (2 m x 0.8 m) consisted of two domestic, oil-filled, electric radiators standing side-by-side. These were covered on the side facing away from the trees with aluminium foil. This maximised the flux of long-wave radiation toward the trees. The cooled surface (2 m x 0.8 m) was formed by two domestic, central-heating radiators, mounted side-by-side on a wooden frame. A water/anti-freeze mixture was circulated through the radiators and a refrigeration unit (Grant Instruments, Cambridge; model FC15) by an electric pump (Grant Instruments; model FH15). The pump unit also contained a heater and thermostat, which could be used to prevent the water temperature from falling below a user-selectable limit. The back of the cool radiators (facing away from the trees), was covered with a layer of expanded

Plate 7.1. The experimental trees located mid-way between cold and hot radiators.

polystyrene and alumiminium foil (plate 7.2). This minimised the heat absorbed by the radiators via convection and radiation.

In an attempt to recreate the 'natural' situation, where large temperature differences do not exist at night, the two surfaces were heated and cooled only between 9:00 and 21:00. This was accomplished by switching the power supply on and off with heavy duty relays, operated by a programmable clock.

At the start of the experiment the young Scots pines possessed only two whorls of branches. Subsequently these are referred to by the years in which their growth commenced (i.e bottom = '1981 whorl', top = '1982 whorl'). One pair of branches was selected in each whorl of each tree, so that the branches were on opposite sides of the whorl and of as similar length as possible. The trees were placed so that one member of each branch pair was adjacent to the heated surface (approximately 15 cm away), and the other close to the cooled surface (approximately 15 cm away). For the duration of the experiment the length of the shoot axis growing from each branch's terminal bud was measured at intervals.

The shoot pairs on one of the Scots pines were selected for detailed measurements of needle extension. Once the needles had attained a length of 1 cm, 10 were chosen near the midpoint of each shoot and marked with a spot of white paint. Their extension was measured at intervals through the growing season.

To aid interpretation of the experimental results some measurements were made to quantify the conditions under which the trees were grown. Air temperature was sensed by a thermistor mounted in a ventilated radiation shield (see sections 5.2.1 and 6.2.1). The temperature of heated and cooled needles of Scots pine were measured with 0.05 mm copper-constantan thermocouples, carefully twisted around the needles. The average surface-to-air temperature differential of four needles on each shoot was determined with four junctions connected in parallel to a reference junction, close to the thermistor bead. The temperature of the cooled surface was also measured with a thermocouple junction referenced to the air. Solar radiation was measured with a solarimeter (section 6.2.3). A CR21 data-logger (section 6.2.4) was used to record readings from these sensors.

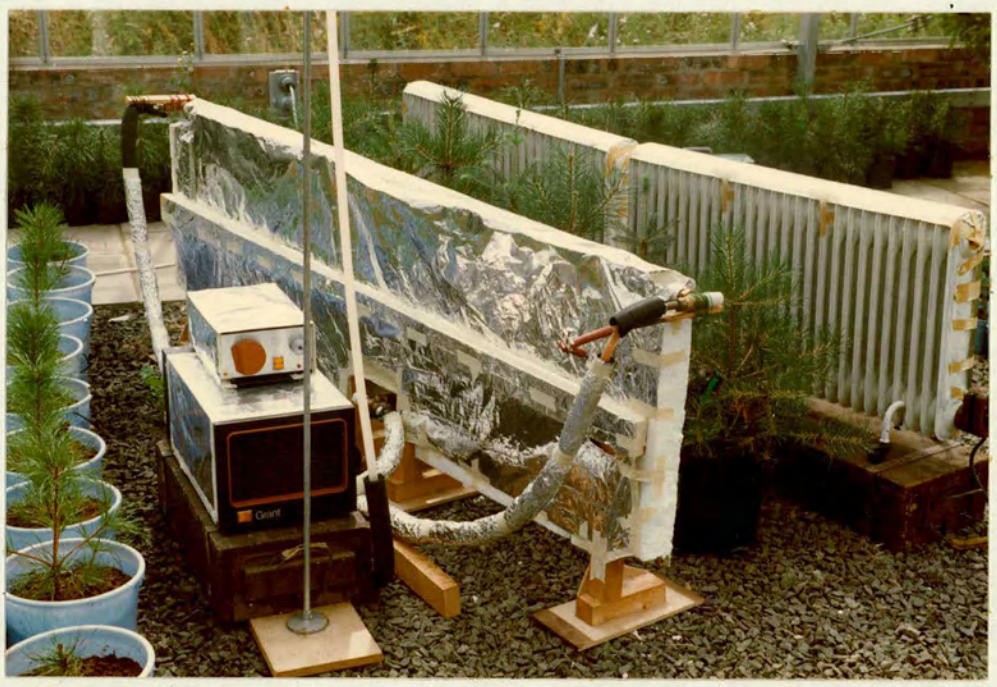


Plate 7.2. Rear view of cold radiator to show the cold bath, the insulated supply pipes and the use of bright foil to minimise radiative heat transfer.

The subsequent extension growth (during 1984) of the terminal buds set by the shoots studied in 1983 was measured, to see if there was any after effect of the temperature treatments.

The analyses of variance and paired sample t-tests, reported below in section 7.4, were calculated using the statistics package, 'PRESTO' (see appendix II).

7.4. Results

The shoots whose extension was followed can be considered to form four groups, or samples, as their growth was affected by both the temperature treatment (heating or cooling) and whorl age (one or two years). The mean extension achieved by each of these samples at various times during the experiment are given in table 7.1 and plotted in figure 7.1. The length data from each set of shoot measurements were subjected to an analysis of variance (single classification) to assess the significance of the differences between the mean lengths achieved by each sample (table 7.2).

The most obvious feature of the data is the difference between the growth rates and final extensions achieved by the shoots of the two different whorls. From 11 June onwards all the inter-whorl length comparisons are statistically significant, the most growth being shown by the 1982 whorl. The temperature treatments did not produce statistically significant differences between the mean lengths of the shoots of each whorl, although in both cases the mean length of the warmed shoots exceeded that of the cooled ones (by 7% for the 1981 whorl and 9% for the 1982 whorl).

The mean needle extensions achieved by each sample are given in table 7.3 and plotted in figure 7.2. The significance of the differences between each sample at each time of measuring were investigated by analysis of variance (single classification). The results of these analyses are given in table 7.4.

The data show that, for needle extension, the effect of the temperature treatments was more pronounced than the effect of the age of the branch. The heated needles showed significantly more growth than the cooled ones,

Table 7.1

Mean lengths of heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four Scots pine measured on various days during 1983.

sample 1: top whorl (1982), cooled (N=4)
sample 2: top whorl (1982), heated (N=4)
sample 3: bottom whorl (1981), cooled (N=4)
sample 4: bottom whorl (1981), heated (N=4)

	Mean shoot length (mm)						
Shoot sample	May 13	May 23	May 27	Jun 4	Jun 11	Jun 19	Jul 5
1	16	56	80	96	106	108	108
2	16	68	93	109	116	117	118
3	15	44	60	67	71	71	72
4	13	52	67	74	75	76	77

Table 7.2

Analyses of variance of lengths of heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four Scots pine measured on various days during 1983. Shoot sample numbers as defined in Table 7.1.

	Probability (only given if significant)						
Shoot sample comparisons	May 13	May 23	May 27	Jun 4	Jun 11	Jun 19	Jul 5
1-2							
1-3				<0.05	<0.05	<0.05	<0.05
1-4					<0.05	<0.05	<0.05
2-3				<0.01	<0.01	<0.01	<0.01
2-4				<0.05	<0.01	<0.01	<0.01
3-4							
Number of cases	16	16	16	16	16	16	16
F-value	0.29	1.00	1.90	4.99	6.23	6.44	6.21
Probability	NS	NS	NS	<0.05	<0.01	<0.01	<0.01

Table 7.3

Mean lengths of needle samples on heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four shoots of a single Scots pine measured on various days during 1983.

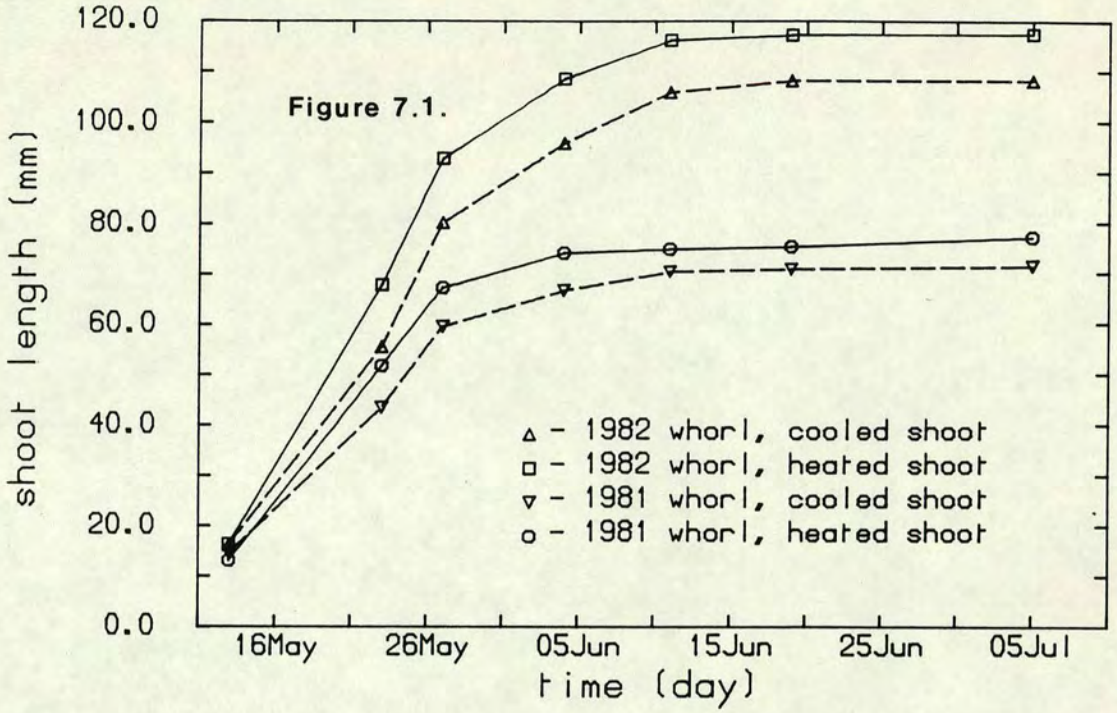
shoot 1: top whorl (1982), cooled (N=10)
shoot 2: top whorl (1982), heated (N=10)
shoot 3: bottom whorl (1981), cooled (N=10)
shoot 4: bottom whorl (1981), heated (N=10)

	Mean needle length (mm)						
Shoot	May 27	Jun 4	Jun 11	Jun 19	Jul 5	Jul 31	Sep 8
1	9	14	20	27	38	55	58
2	13	19	26	34	49	68	71
3	11	16	23	30	41	58	65
4	16	23	32	41	56	74	79

Table 7.4

Analyses of variance of lengths of needle samples on heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four shoots of a single Scots pine measured on various days during 1983. Needle sample numbers as defined in Table 7.3.

	Probability (only given if significant)						
Needle sample comparisons	May 27	Jun 4	Jun 11	Jun 19	Jul 5	Jul 31	Sep 8
1-2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
1-3	<0.05	<0.05	<0.01	<0.001	<0.001	<0.001	<0.001
1-4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2-3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2-4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
3-4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Number of cases	40	40	40	40	40	40	40
F-value	59.5	70/2	107/3	170.2	310.6	257.7	185.4
Probability	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001



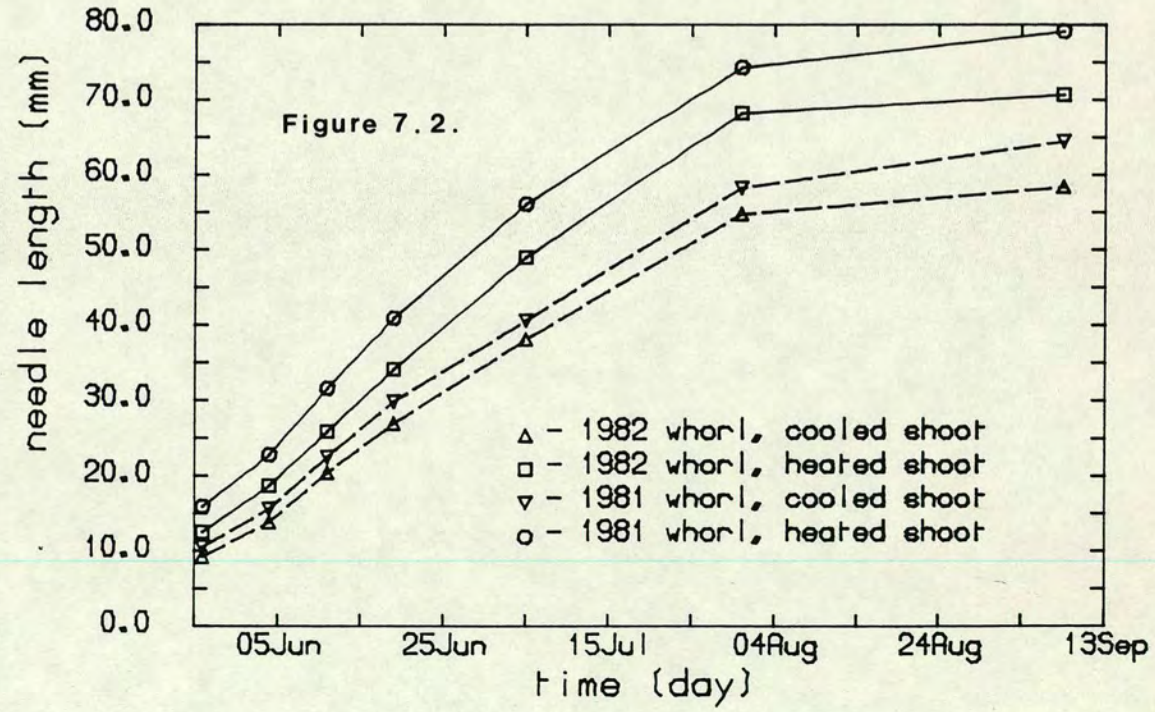


Figure 7.1. Progress of shoot length for shoots on whorls formed in 1981 and 1982, all measured in 1983.

Figure 7.2. Progress of needle length for shoots on whorls formed in 1981 and 1982, all measured in 1983.

irrespective of the whorl occupied by the branches sampled. In both whorls the heated needles achieved mean lengths 22% greater than those achieved by the cooled ones.

The temperature and solar radiation measurements made on two days are presented in figure 7.3 (27 August 1983) and figure 7.4 (28 August 1983). On both days the levels of solar radiation were moderate and fluctations resulted from the passage of clouds overhead. The temperatures of the air, the cooled needles and the refrigerated surface are clearly affected by the amount of solar radiation. There is a strong correspondence between peak values of these temperatures and peak values of radiation. The heated needles were generally about 5 °C to 7 °C warmer than the cooled ones; their temperature was subject to regular oscillations, most probably caused by the operation of the thermostats of the oil-filled heaters. The cooled needles were between 0 °C and 2 °C less than air temperature.

The extension data resulting from the two sets of measurements made in 1984 are given in table 7.5. Analyses of variance were performed to assess the significance of the observed differences between the shoot samples (table 7.6).

At the beginning of 1984's extension growth (measurements of 10 May), before bud burst had occurred, the buds set by the previously heated shoots were longer than those of the previously cooled shoots in the same whorl. As found previously in 1983, the shoots of the younger whorl achieved the greater final extensions (measurements of 16 October), although not all the inter-whorl comparisons were statistically significant. In both whorls, the shoots that had been heated in 1983 extended more than those that had been cooled (although the difference was only significant for the 1982 whorl). For the 1982 whorl the length advantage of the previously heated shoots was 25%, and for the 1981 whorl it was 29%.

The 1984 data were re-analysed by means of paired sample t-tests, thus taking advantage of the initial pairing of heated and cooled shoots to remove the variability in extension caused by differences between whorls and trees. The results are given in table 7.7. The differences between the extensions of the previously heated and cooled shoots were highly significant on both days when measurements were made.

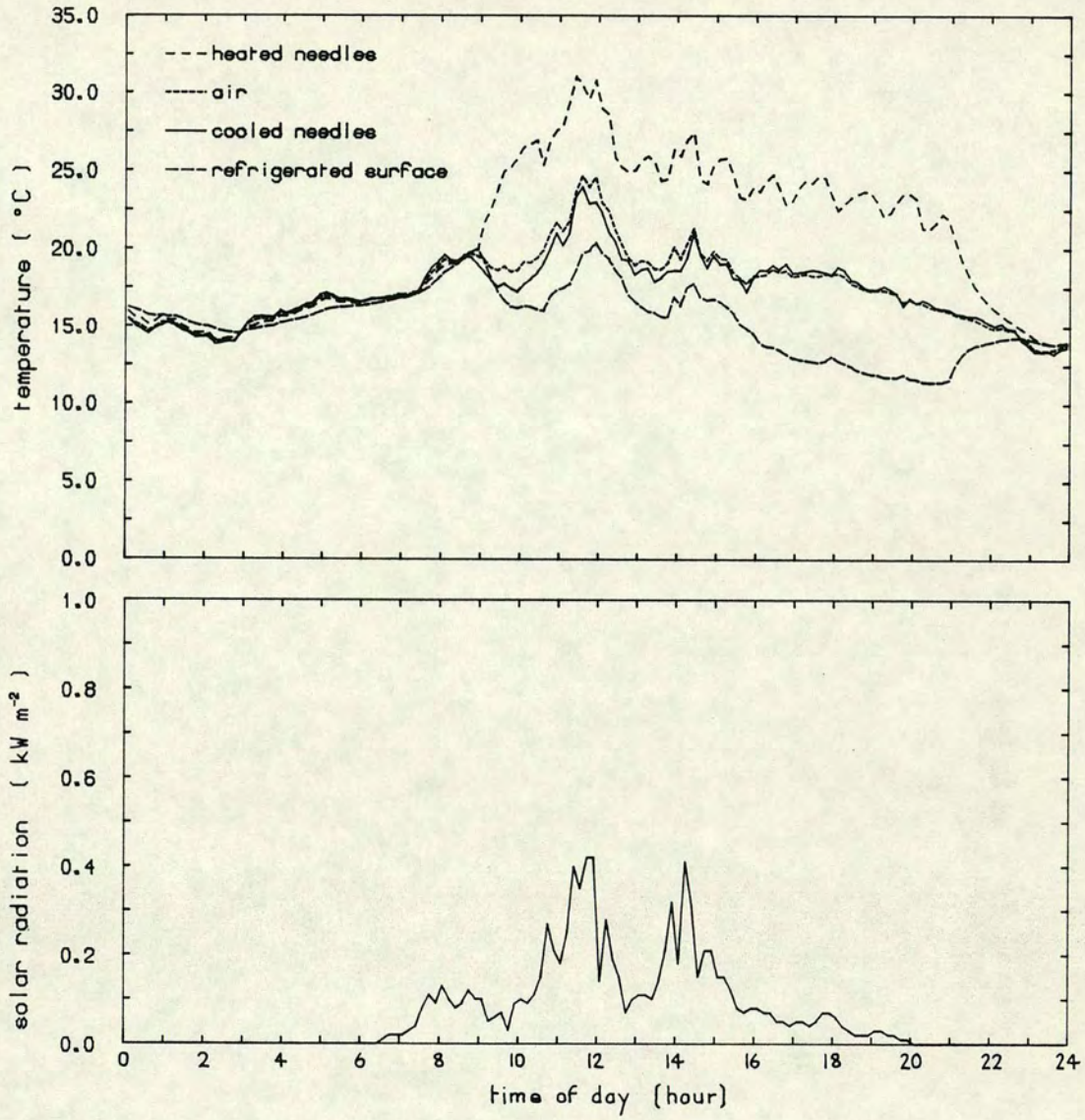


Figure 7.3 Performance of the radiative heat transfer unit on 27 August 1983.

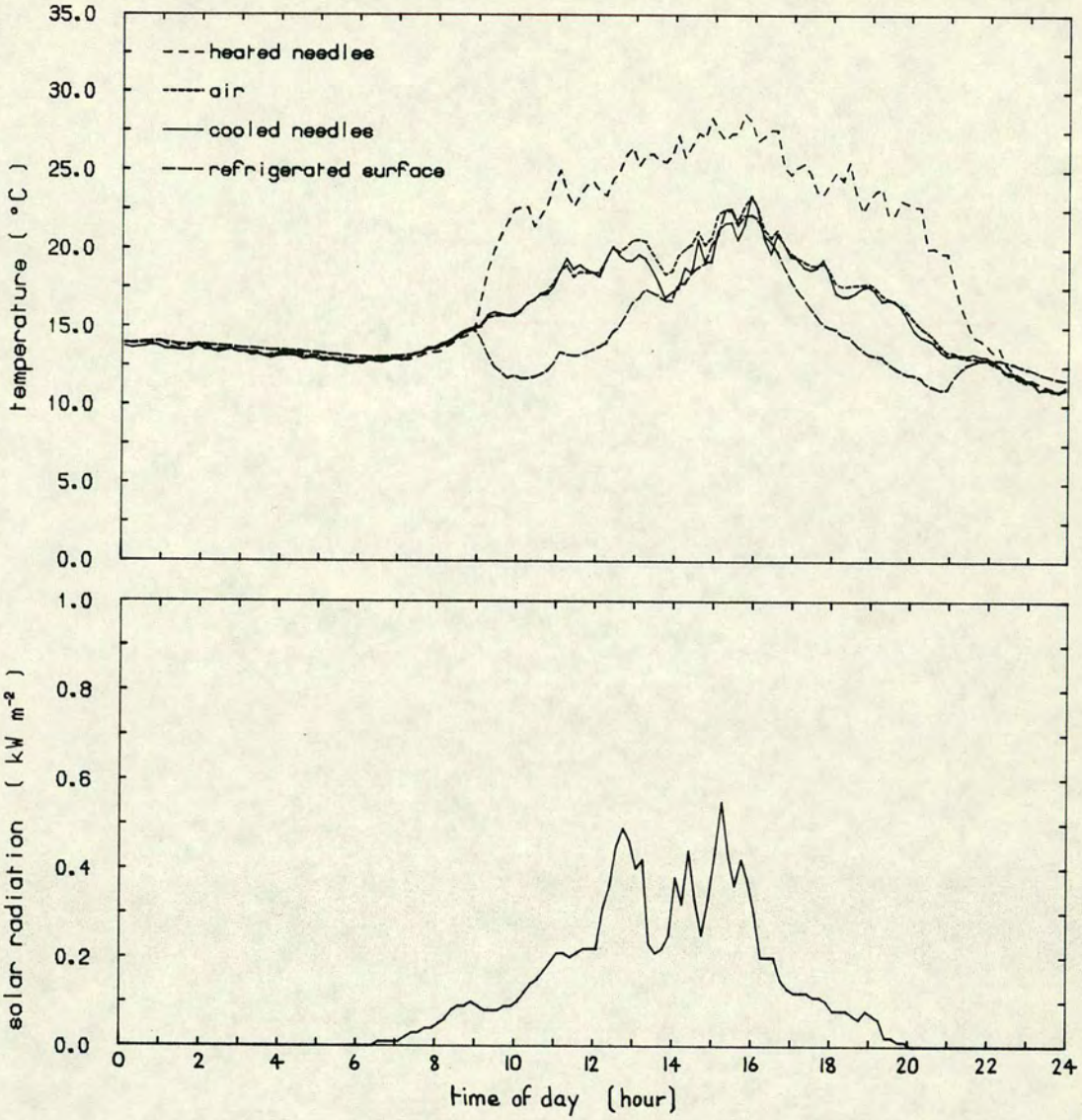


Figure 7.4 Performance of the radiative heat transfer unit on 28 August 1983.

Table 7.5

Mean lengths of previously heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four Scots pine measured on two days during 1984 (the year after the heating/cooling treatments were applied).

sample 1: top whorl (1982), cooled (N=4)
sample 2: top whorl (1982), heated (N=4)
sample 3: bottom whorl (1981), cooled (N=4)
sample 4: bottom whorl (1981), heated (N=4)

	Mean length (mm)	
Shoot sample	May 10	Oct 16
1	11.5	101
2	14.5	135
3	9.0	70
4	11.3	90

Table 7.6

Analyses of variance of length of previously heated and cooled shoots in greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four Scots pine measured on two days during 1984 (the year after the heating/cooling treatments were applied).

	Probability (only given if significant)	
Shoot sample comparisons	May 10	Oct 16
1-2		<0.05
1-3		
1-4		
2-3	<0.01	<0.01
2-4	<0.05	<0.05
3-4		
Number of cases	16	16
F-value	4.82	6.27
Probability	<0.05	<0.01

Table 7.7

Paired sample t-tests of the differences in length between heated and cooled shoots in a greenhouse investigation of the effect of an artificial temperature gradient on shoot extension; data from four Scots pine measured on two days during 1984 (the year after the heating/cooling treatments were applied). Standard errors shown in brackets.

Temperature treatment	Number of shoots	May 10: mean shoot length (mm)	Oct 16: mean shoot length (mm)
Heated	8	12.9 (1.0)	113 (12)
Cooled	8	10.3 (0.7)	85 (9)
Mean of differences		2.6	28
t-value		6.25	4.71
Probability		<0.001	<0.01

7.5. Discussion

The artificial temperature gradient applied to the trees during the experiment did cause asymmetrical growth to occur. The warmed shoots extended more rapidly and achieved greater final lengths than the cooled ones. The growth rates and final extensions of the needles were also greatest for the heated shoots. Considering the size of the temperature difference applied, however, its affect on shoot elongation was relatively small. Although a similar difference does occur at times in the natural environment, it would only exist for part of the time. Thus the treatment applied would be expected to produce an asymmetry at least as great as that observed in the field; this was not the case.

The failure of the treatment to produce a larger effect might result from differences in shoot water status. The hotter shoots would certainly have experienced a greater leaf-to-air vapour pressure difference than the cool ones, favouring a higher evaporation rate. It is, however, considered unlikely that this would have caused the heated shoots to experience water potentials low enough to reduce the rate of extension. The trees were kept well watered, and the observation of the beneficial effect of heating on needle extension suggests that the warmer shoots were not water stressed.

A more probable explanation is that the relatively minor effect of the treatment results from the absolute temperatures experienced by the heated and cooled shoots. Although the temperature difference applied was of an ecologically realistic magnitude, the absolute temperatures experienced by the shoots were rather unrealistic. During the experiment the temperature of the cooled shoots was mostly in the range 15 °C to 25 °C, while the temperature of the heated shoots was usually between 20 °C and 30 °C. At the exposed sites, where wind-shaped trees naturally occur, a rather different temperature regime is experienced during the growing season. The exposed shoots experience daytime temperatures mostly between 10 °C and 15 °C and the sheltered shoots 10 °C to 25 °C, their temperature advantage depending on wind speed and net radiation. Hellmers (1962) reported studies of the effect of temperature on the growth of several conifer species. These studies investigated the growth responses of one-year-old seedlings to temperature in controlled environment chambers. For Jeffrey pine (*Pinus jeffreyi*) the optimum temperature for dry weight production was 15 °C and for Aleppo

pine (*Pinus brutia*) it was 20 °C. The optimum temperature for stem elongation in eastern hemlock (*Tsuga canadensis*) was also 20 °C. These results suggest that the heated Scots pine shoots (usually between 20 °C and 30 °C) probably experienced supra-optimal temperatures for much of the time; instead of promoting growth, the heating treatment must have often retarded it. For some proportion of the time, depending on the exact temperature optimum for shoot growth in Scots pine, the cooled shoots must have been closer to the optimum temperature than the heated ones, thus reducing the expected effect of the temperature difference on shoot extension.

It proved to be technically difficult to simulate the natural temperature regime. The greenhouse used for the experiment was poorly ventilated, so that air temperatures of 25 °C were often achieved on sunny days. The principle of controlling the shoot temperatures by radiative coupling to controlled temperature surfaces was sound enough, and had the advantage of minimal interference (i.e. nothing had to be attached to the shoots). For the method to be really effective in simulating natural conditions the cooled surface should have been cooled to a much lower temperature. In fact, the best arrangement would have been to completely discard the heater and keep one side of the trees close to a highly-refrigerated surface. Unfortunately, a more powerful refrigeration unit was not available.

A further problem with the experiment arose from the lack of replication. It was only possible to apply the treatment to a small number of trees, because of the limitation imposed by the size of the controlled temperature surfaces. If the growth of a larger sample of trees had been investigated, the differences in extension that were observed might have been statistically significant.

It is interesting to note that the asymmetry of the shoots' growth was greater in the year after the treatment than during it. The warmed shoots appear to have set larger buds at the end of the 1983 growing season than the cooled ones. This alone does not, however, explain the greater extension achieved in 1984 by the previously-warmed shoots, as the observed asymmetry in extension at the end of the 1984 growing season was greater than that observed at the beginning. The implication is that not only were the buds of the previously-heated shoots larger at the start of the 1984 growing season, they also extended more rapidly than those of the previously-cooled

shoots.

The behaviour of the Scots pine trees in this experiment agrees well with the observations of Mikola (1962). He studied the growth of Scots pine in Finland, and found that radial growth and needle extension were affected by the temperature of the current season, while height growth was primarily affected by the temperature of the previous summer. The latter observation is explained by the fact that the number of needles on a shoot is predetermined in the bud, which is formed during the previous summer, and the length achieved by a shoot depends mainly on the number of needles it bears. Dendrochronological studies (Fritts, 1976) also find a strong correlation between ring width and mean summer temperature of the current and previous years.

The results of this experiment suggest that the growth of different parts of the same individual are influenced most strongly by the temperatures they experienced in the preceding growing season. Thus, if the sheltered side of a tree experiences large temperature excesses rather frequently during a particular summer, its extension growth will benefit in the following year.

CHAPTER 8
CONCLUSIONS

The review of published work (chapter 1) shows that the wind-shaping of trees is undoubtedly a complex phenomenon, in which a variety of processes have been implicated. Much of this work simply describes or quantifies the form of wind-shaped trees, or is rather speculative in nature. The objective of this study was to achieve a greater understanding of the underlying processes involved in wind deformation, by means of detailed field observations and experiments. The results have been presented and discussed in the preceeding chapters. This, the concluding chapter, is an attempt to link these results to construct a unified picture of the wind deformation of conifer trees.

The breakage of shoots by the wind is the most obvious process involved in wind-shaping. The study of Sitka spruce at Dunslair Heights (chapter 2) confirmed its importance. Over a four year period half of the sample of branches were broken or lost their terminal shoots. It was found that during storms, only those shoots facing directly into the wind were broken. Thus, at a site where one wind direction is truly prevalent, the windward side of a tree's stem becomes partially or totally denuded of branches as the years progress.

Most of the damage to the Sitka spruce trees occurred during the summer, when the new shoots are fragile and thus vulnerable to breakage. A critical phase for shoot breakage was identified. This occurs at the end of the period of shoot extension, when the shoots have achieved their full size, thus experiencing maximum drag forces when the wind blows, but are still mechanically weak as the process of lignification has only just begun.

The loss of branches from the windward side of trees clearly contributes strongly to the asymmetrical crown shapes typical in windswept areas. The observations at Dunslair Heights showed that another mechanical effect, the wind induced bending of branches, is also very important. The spruce branches tended to become curved over the four year study period, so that their apices pointed away from the prevailing wind direction. Observations of the positions adopted by flexible new shoots when the wind blew over the trees, and the experiment reported in chapter 3, supported Putnam (1948), who

suggested that wind shaping is caused by shoots becoming permanently fixed in a swept back configuration by lignification, as they are held by the force of the wind.

The amount of permanent branch curvature was found to be related to branch position, the branches originating on the side facing the prevailing wind direction being swept back by 70°, on average. The branches on the sheltered side exhibited little or no curvature. Thus the branches on the windward side that are not broken by the wind become swept back to the leeward. This makes an important contribution to the uneven distribution of foliage that is characteristic of wind-deformed trees.

The measurements of the extension of spruce shoots at Dunslair Heights (chapter 4) showed that the sheltered shoots achieve greater lengths by the end of the growing season than the exposed ones. So not only are branches lost from the exposed side or swept to leeward by wind induced curvature, but the sheltered branches achieve greater lengths than those on the windward side. This greatly enhances the crown asymmetry arising from shoot breakage and wind-induced bending.

The observed differences in the annual length increments of branches resulted from differences in growth rates and initial bud sizes, the sheltered shoots extending more rapidly, and setting larger buds. As the rate of shoot extension and the development of buds are known to be primarily influenced by temperature (see chapter 1), it was suggested that the more rapid growth of the sheltered side might be a response to the occurrence of generally higher temperatures. Consideration of the energy balance of shoot apices (chapter 5) showed that the leeward shoots are liable to experience higher temperatures as a result of the shelter afforded by the rest of the tree's foliage. The experiment described in chapter 7, despite technical difficulties in simulating a realistic temperature regime, showed that for Scots pine the warming of one side resulted in greater extension growth of the branches on that side. In order to firmly establish a causal link between temperature differences and asymmetrical branch growth, similar experiments should be performed for other species. Care should be taken to ensure that the heated and cooled shoot apices are kept at ecologically realistic temperatures, closely simulating those experienced on the sheltered and exposed sides of a

wind-deformed tree.

The field measurements of temperature, reported in chapters 5 and 6, ascertained that significant differences in temperature do sometimes exist between the apices of exposed and sheltered shoots. For Arolla pine in Austria, the greatest difference observed was 4°C. Optimum conditions of high net radiation and low windspeed were not encountered during the study, so it is likely that larger temperature differences occur sometimes.

During the much longer series of measurements made at Dunslair Heights, large temperature differences (up to 5°C) were found to occur under optimum conditions, but for much of the time the temperature differences were smaller or non-existent. When long term averages were calculated, the differences between the means for the exposed and sheltered shoots apices seemed to be too small to cause much difference in growth rates.

Nevertheless, temperature differences still provide the most likely explanation for the observed differences in shoot extension rates. The impression given by the calculated means may be incorrect, as it implicitly assumes that a linear relationship exists between extension rate and temperature, and that this relationship is time independent. It is known that the rate of extension is most sensitive to temperature during the early phase of shoot elongation; the first few weeks of active extension were unfortunately not included in the period of measurements made at Dunslair Heights. Furthermore, had an older whorl, with more foliage to afford shelter to the leeward shoot apices, been selected for the measurements, it is probable that larger temperature differences would have been observed.

Thus, it is likely that temperature differences between the sheltered and exposed sides of trees do play a general role, via growth rates, in wind-shaping. Determination of the relationships between boundary layer resistance and ambient wind speed for spruce shoots of differing exposure showed that the leeward shoots do 'benefit' (in terms of their boundary layer resistances) from the shelter they experience; the resistances of the sheltered shoots were at least three times those of the exposed shoots. Arolla pine has much denser foliage than Sitka spruce, so the shelter experienced by the leeward pine branches is likely to be greater. In the alps less mist and rain occur during the summer than in Scotland, so the high levels of net radiation

that favour temperature differences are experienced more frequently. It is regrettable that it was not possible to make long term measurements in the alps, as the short term investigation at Mt. Patscherkofel suggested that larger long term temprature differences would have been observed than at Dunslair Heights.

To summarise, the following picture of the wind-shaping of the spruce trees at Dunslair Heights has emerged. Shoot breakage during the growing season, wind induced curvature and more rapid elongation of the sheltered branches, probably as a result of greater warmth, are all key processes. The windward side of the stem is partially denuded by the breakage of shoots and those that remain form branches that become permanently swept to leeward. The more rapid growth of the sheltered shoots, resulting in longer leeward branches, enhances the asymmetry established by the pattern of branch distribution resulting from breakage and bending.

The other processes thought to be involved in wind-shaping of trees (introduced in chapter 1) are likely to be important for other conifer species at different geographical locations. Winter desiccation of exposed shoots, resulting from incomplete maturation of the cuticle (the 'winter browning' of Tranquillini, (1974)) or cuticular damage by wind-borne ice or soil (Daubenmire, 1959; Grace, 1977) appear to be important at high altitudes on mountains with continental climates. Here too, the winter-time breakage of branches caused by the accumulation of ice glaze (Lawrence, 1939; Marchand, 1980) seems to play a large role in wind deformation. At Dunslair Heights the winters were relatively mild, so none of these processes were observed. In the future the application of similarly detailed, long term study methods to trees growing in locations where particularly harsh winters are experienced would provide interesting information that could usefully be contrasted with the results of the present study.

The growth retarding effects that have been demonstrated for mechanical perturbation of trees and herbaceous plants were not investigated during this study. The possible role of wind-induced shaking in inhibiting the growth of the windward branches is not discounted and is certainly worthy of study, although it does not seem to be easily amenable to experimental investigation.

The processes found to be active in the wind-shaping of the spruces at

Dunslair Heights are certainly involved in the wind deformation of other conifer species at other sites, but their relative importance is likely to vary widely. It seems reasonable to speculate that factors such as the nature of the climate, particularly the strength of the winds experienced, and the tree species, will influence the relative importance of the wind-shaping processes.

In very exposed localities, where mean annual wind speeds are particularly high, shoot breakage is probably the most dominant process. The true 'flag trees' observed at such sites do not possess any branches, except those immediately to the lee of the stem, which form a vertical plane of foliage. Wind-induced curvature is of little importance, as it is the windward branches (which in this case are non-existent) which are affected by this process. The distribution of temperature throughout the canopy is likely to be uniform for most of the time. This results from the low degree of shelter afforded by the planar canopy and the fact that at high ambient wind speeds, even 'sheltered' shoot apices have a low boundary layer resistance, so their excess temperature above air is always small, even if net radiation is high. This is clearly shown by the temperature data from Dunslair Heights. On very windy days, even when it was clear and sunny, both the exposed and sheltered shoot apices were close to air temperature.

In less exposed localities, wind-induced curvature and asymmetrical growth caused by temperature differences are probably more important than breakage in effecting wind deformation.

The daily variation in wind speed will also influence the relative importance of shoot breakage and wind-induced curvature. Consider two sites with similar mean annual wind speeds, but different temporal patterns of wind strength. At the site where there is a constant moderate wind, but storms occur rarely, wind-induced bending of branches will be favoured, particularly if fairly strong winds persist during the critical phase identified in chapter 3. At the other site, where wind speed fluctuates more widely, shoot breakage will be favoured by the higher frequency of gales, even if the wind is only light or moderate for most of the year.

Temperature differences between the exposed and sheltered sides of trees are likely to be particularly effective in causing asymmetrical growth in places where the summers are cold, for example close to the tree line and the

latitudinal limit of tree growth in the far north. A few extra degrees of warmth experienced by the sheltered shoots would greatly benefit their growth in such localities, where the period of time that ambient temperatures are above the threshold for growth is barely long enough to permit survival.

Tree species vary in the degree of their response, in terms of canopy deformation, to the strength of the prevailing wind. This was clearly shown by the survey of a wide variety of north american conifers made by Wade and Hewson (1980). Noticeable variation is apparent in the quantitative relationships ('calibrations') between mean annual wind speed and degree of canopy deformation that were established for the different species. This variation must reflect mechanical, morphological and possibly phenological differences between species. For instance, in the present study the difference in the sizes and packing of the needles of Sitka spruce and Arolla pine has been noted and the effect of this difference on shelter factor, and hence temperature gradients, discussed. As a further example, it is interesting to consider the possible effects of the difference between the process of shoot growth in spruces and pines. In spruces the needles are quite well developed at bud-burst, and they continue to grow as the shoot axis elongates. In pines the needles are not visible at the time when the bud scales separate; they only begin to grow when elongation of the shoot axis is nearly complete. The presence of needles on the spruce axes during extension must make them more vulnerable to breakage by the wind than the pine shoots, as a greater surface area is presented to the wind at the time when the shoots are mechanically weak.

The scope of this thesis has necessarily been limited by the desire to make detailed investigations, by long term field studies and controlled experiments, of some of the hypothetical wind-shaping processes. There is a need for similar intensive studies, perhaps over longer time periods, of other species at sites where different climatic conditions are experienced. The resulting information from such studies would aid those involved in the afforestation of exposed, upland sites, the planning of shelter belts and the execution of wind-power surveys. It would also allow the formulation of wide-ranging general principles concerning the deformation of trees by the wind.

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APPENDIX I

LIST OF SYMBOLS

C	convective heat loss (W m^{-2}).
C_p	specific heat capacity of air at constant pressure (J $kg^{-1}{}^{o}C^{-1}$).
d	dimension of flat plate parallel to flow (m).
E	evaporation rate (kg $m^{-2}s^{-1}$).
G	conduction of heat to plant body (W m^{-2}).
N	sample size.
P	rate of energy use in photosynthesis (W m^{-2}).
r_a	boundary layer resistance to heat transfer (s m^{-1}).
R	net radiation (W m^{-2}).
S	rate of heat storage (W m^{-2}), Solar irradiance (W m^{-2}).
T_a	air temperature (°C).
T_s	bud surface temperature (°C).
ΔT	temperature difference (°C).
u	windspeed (m s^{-1}).

Superscripts

ex	Quantity referred to is for exposed shoot.
sh	Quantity referred to is for sheltered shoot.

Greek symbols

ΔT	temperature difference (°C).
κ	thermal diffusivity of air (m^2 s^{-1}).
λ	latent heat of vaporization (J kg^{-1}).
ν	kinematic viscosity of air (m^2 s^{-1}).
ρ	density of air (kg m^{-3}).

APPENDIX II

COMPUTER SOFTWARE ACKNOWLEDGEMENTS

Details of the computer packages used for data analysis and presentation in this thesis.

i) Presto
Author R.I.Muetzelfeldt.
Reference Available from the author at the Department of Forestry and Natural Resources, University of Edinburgh, EH9 3JU.

ii) Easygraph
Graphics package.
Author N.Stroud (originator W.A.Watson).
Reference User Note 12, Edinburgh Regional Computing Centre, J.C.M.B., Kings Buildings, Mayfield Road, Edinburgh.

iii) MSU, C20
Programs for transfering data from the mass storage unit and the cassette recorded output from the Campbell CR21 datalogger, to the university mainframe computer.
Author A.P.Sandford.
Reference Available from the author at the Department of Forestry and Natural Resources, University of Edinburgh, EH9 3JU.

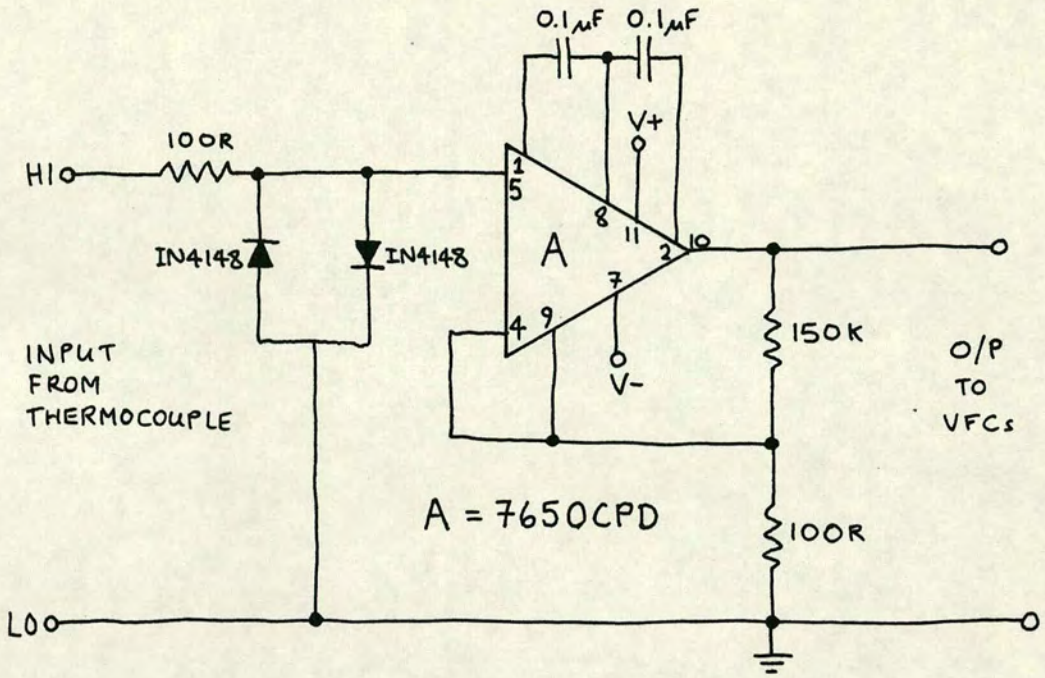

Figure AIII.1. Input amplification stage of integrator circuit used with each thermocouple set.

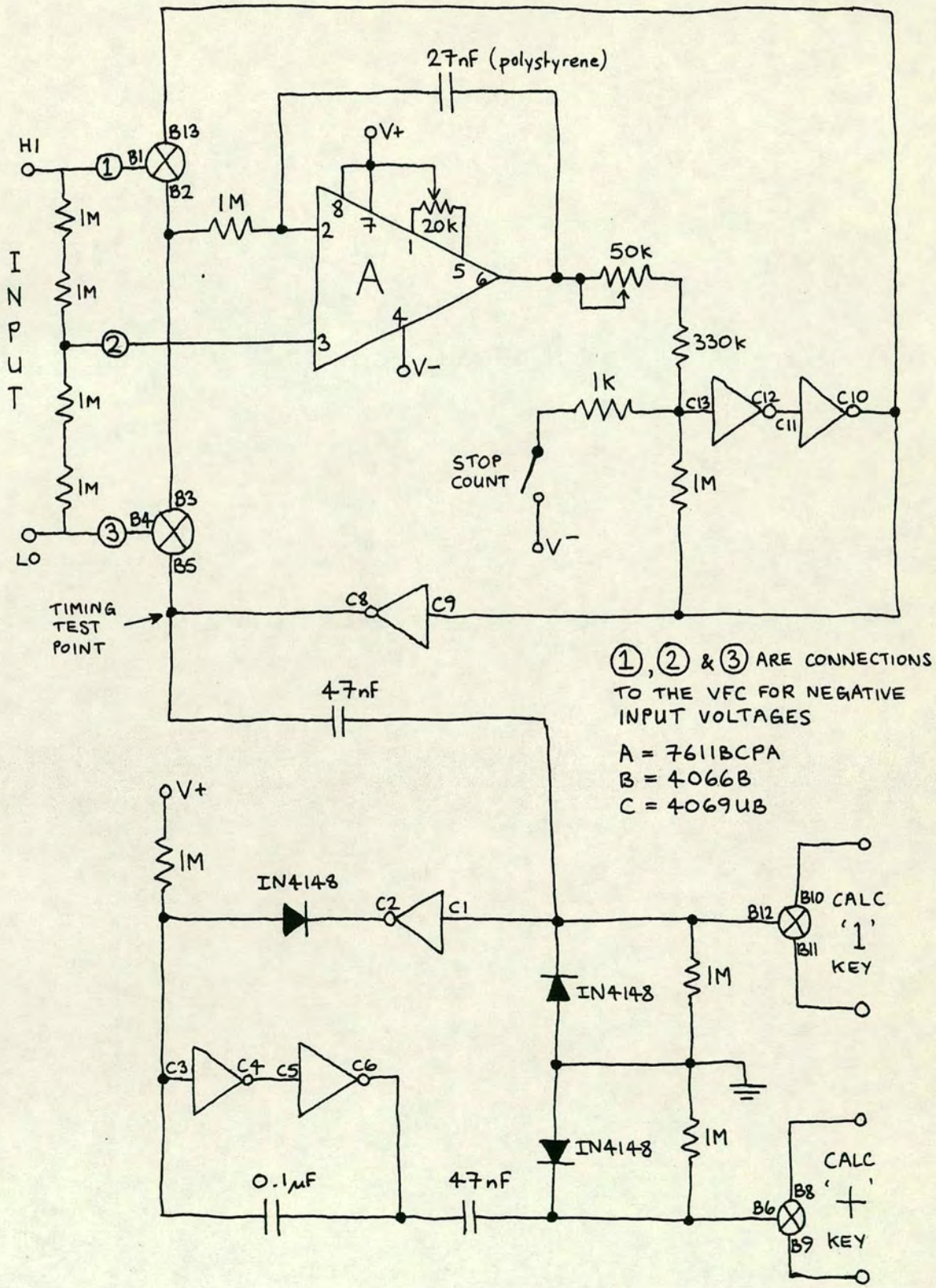

Figure AIII.2. Voltage to frequency converter and calculator driver circuit for positive input voltages (see section 5.2.4.). The input of this circuit is connected to the output of the circuit shown in figure AIII.1.

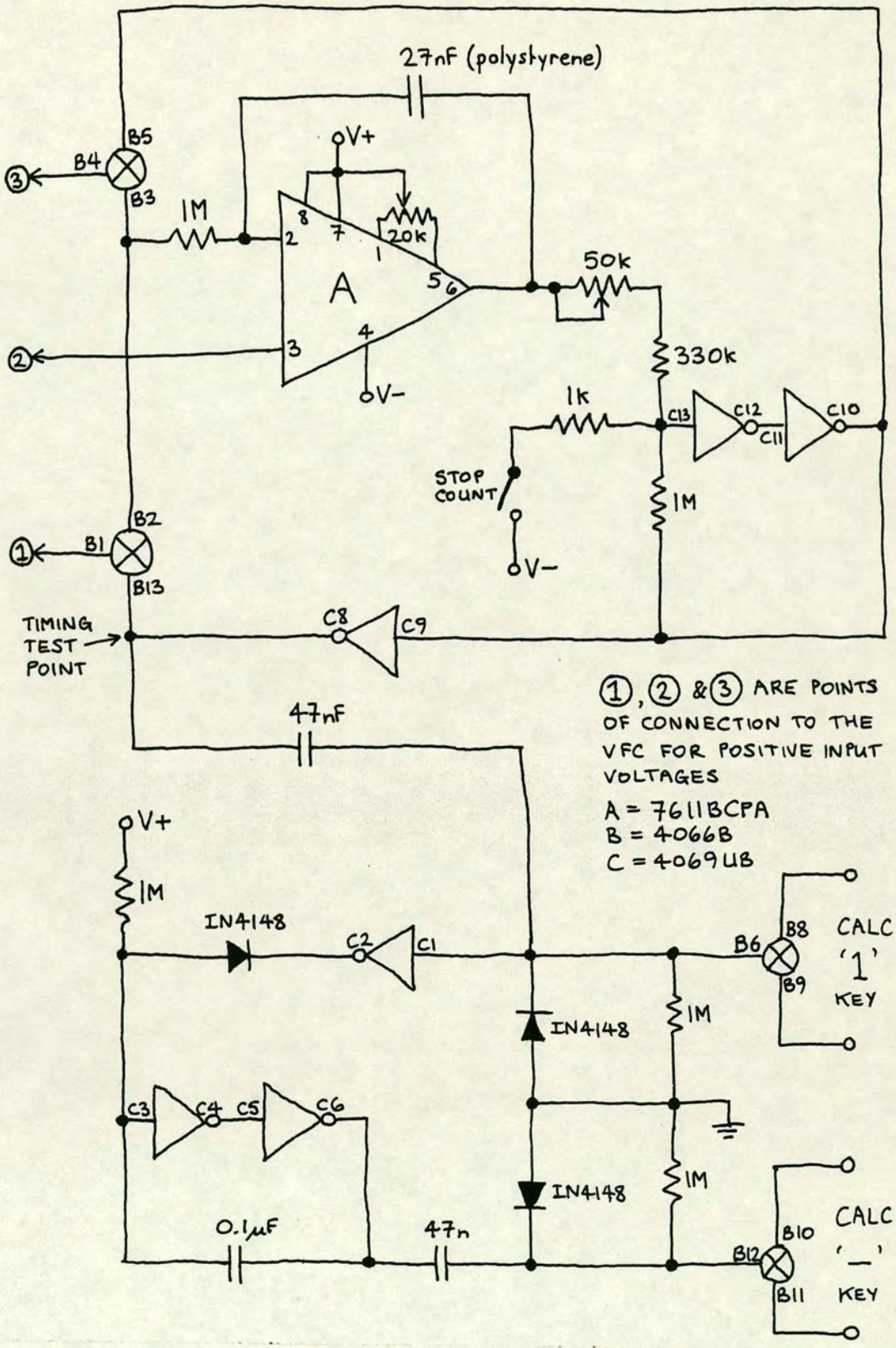

Figure AIII.3. Voltage to frequency converter and calculator driver circuit for negative input voltages (see section 5.2.4.). This circuit is connected, as indicated, to the circuit shown in figure AIII.2.

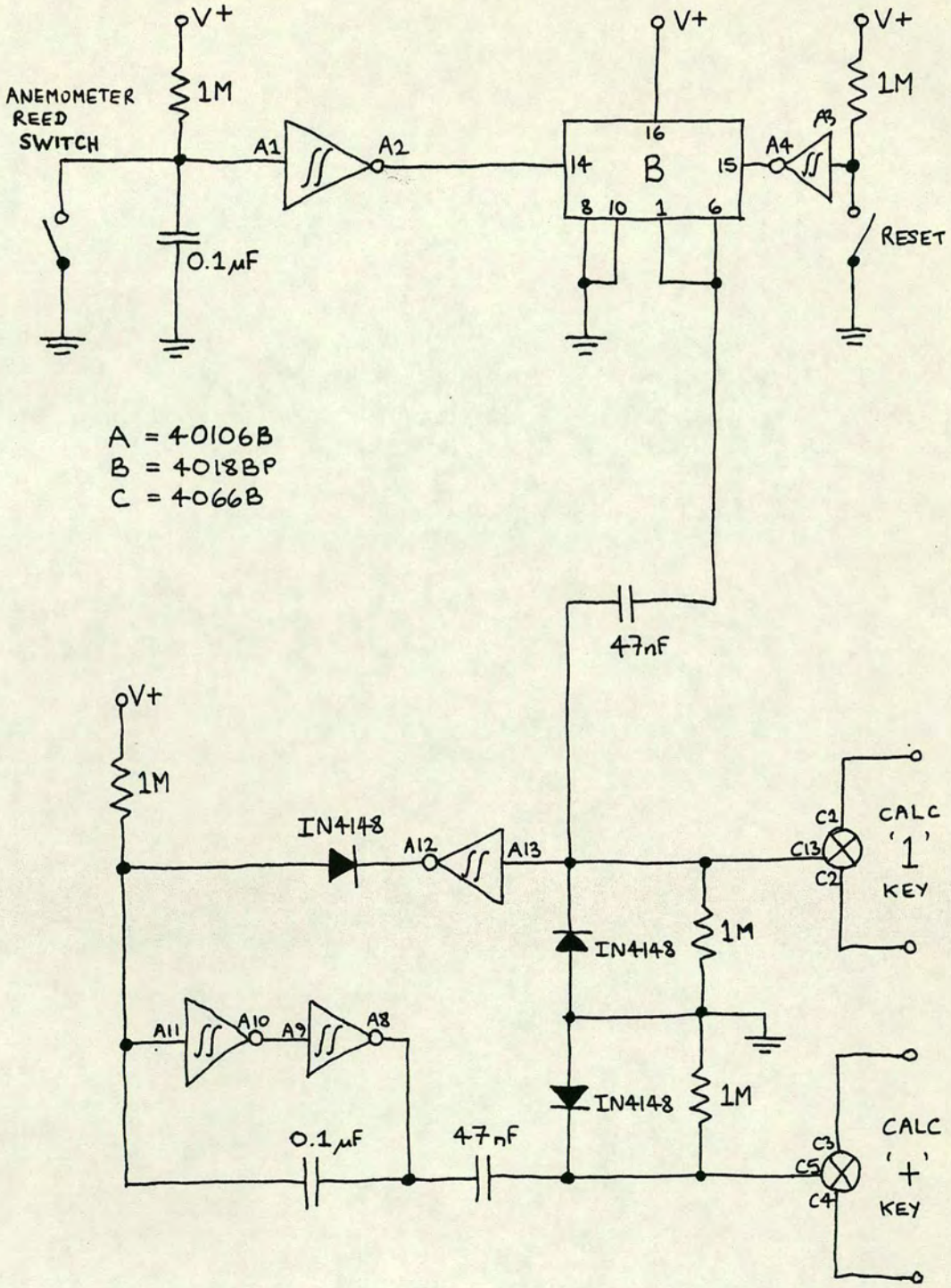

Figure AIII.4. Divide-by-6 contact-closure counter and calculator driver circuit used to count rotor revolutions of the Vector Instruments A100R cup anemometer (see section 5.2.4.).

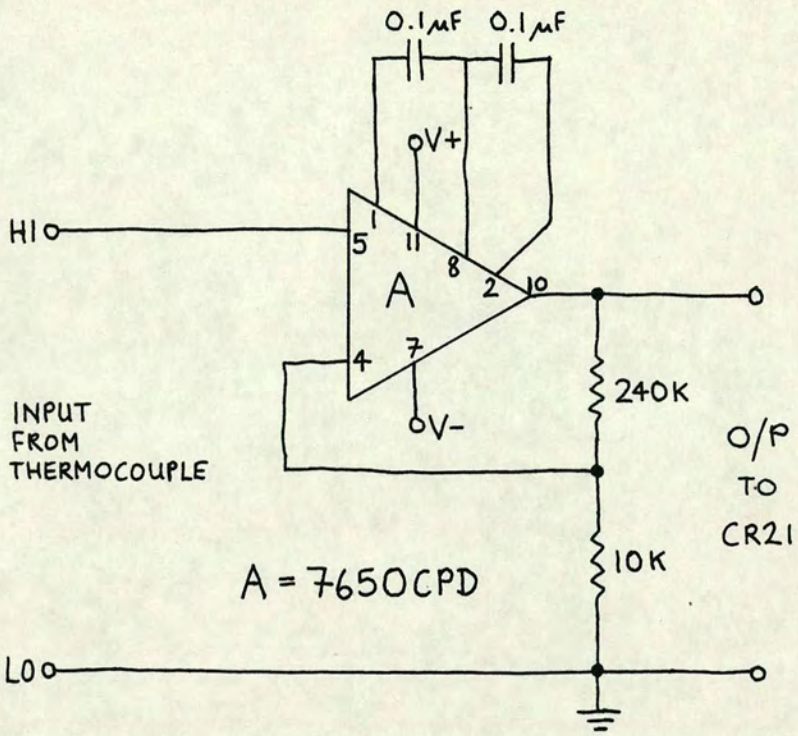

Figure AIII.5. Amplifier circuit used to interface each thermocouple set with one of the CR21's analogue input channels (see section 6.2.1.1.).

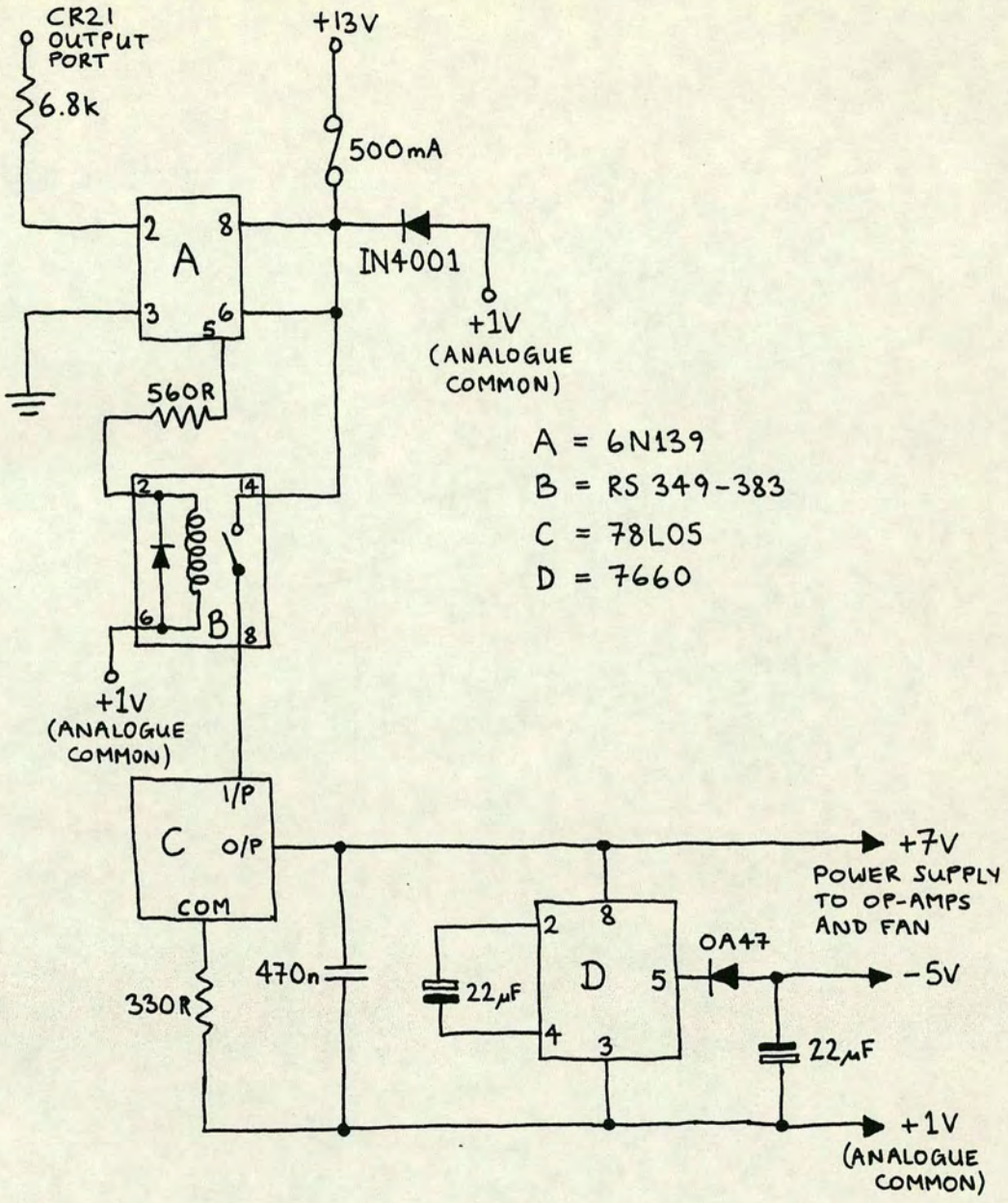

Figure AIII.6. Circuit used to allow switching of the battery supply to the temperature unit (see section 6.2.1.1.) by one of the CR21's output ports (5V = on, 0V = off).